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San Diego

**Growth and reproduction of female short-beaked common
dolphins, *Delphinus delphis*, in the eastern tropical Pacific**

A thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science in Marine Science

by
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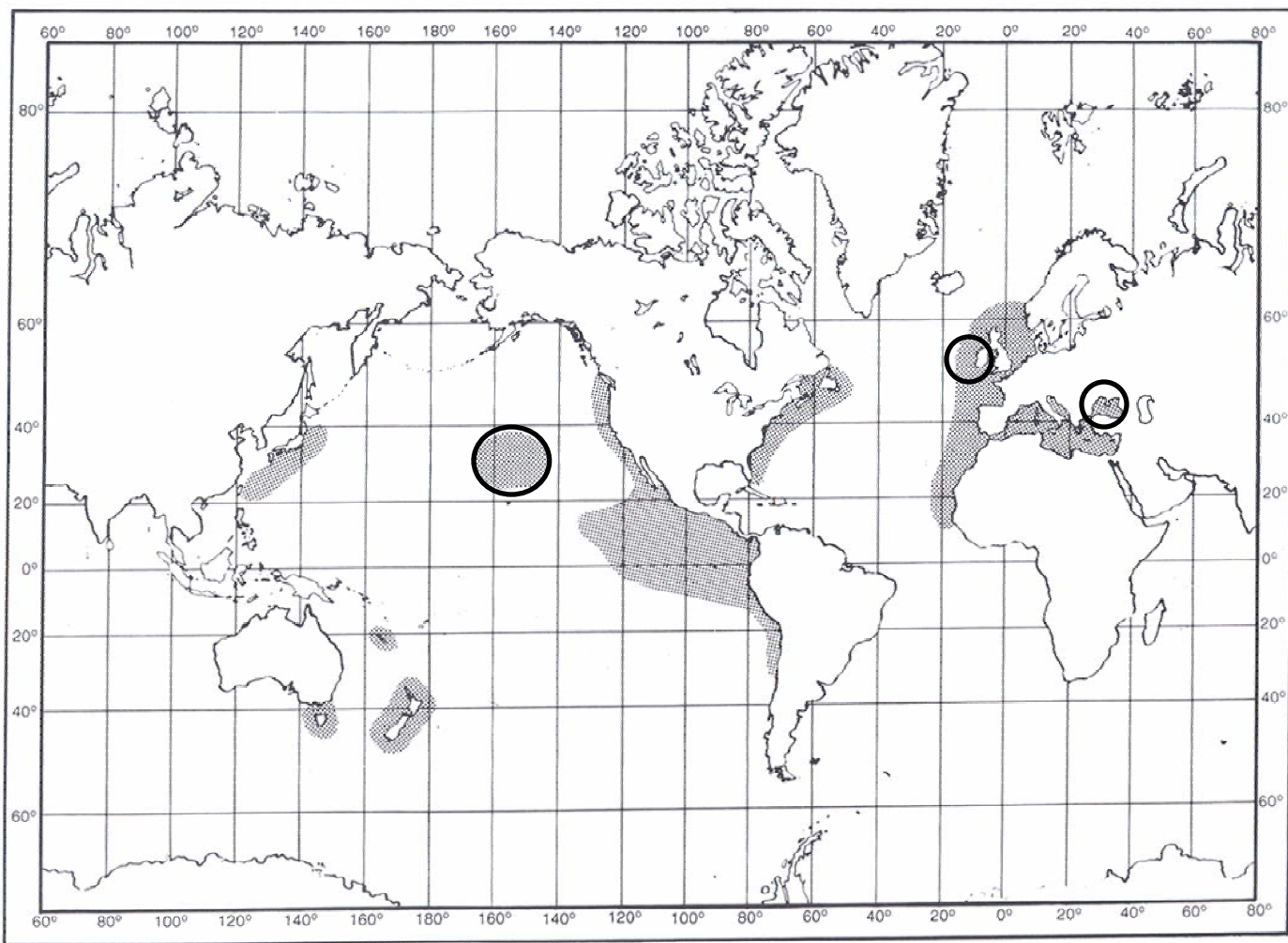
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CHAPTER 1: GENERAL INTRODUCTION

Short-beaked common dolphins, *Delphinus delphis*, are distributed worldwide in temperate, tropical, and subtropical seas (Figure 1) and occupy near-shore coastal waters as well as habitats thousands of miles from shore (Heyning and Perrin 1994). Comprehensive studies on the growth and reproduction of this species have been completed for populations in the North Pacific, Northeast Atlantic, and the Black Sea (Figure 1). This study will focus on the population living in the eastern tropical Pacific (ETP) and compare the results with those from the N. Pacific.

D. delphis are impacted by fisheries worldwide (Hobbs and Jones 1993; Evans 1994; Perrin et al. 1994; Tregenza and Collet 1998). In the ETP, incidental mortality of *D. delphis* occurs in the tuna purse-seine fishery. In the late 1950s, the purse-seine fishery began to replace the pole-and-line fishery for tuna in the eastern Pacific Ocean (Perrin 1969). The new fishery encircled herds of dolphins of the genera *Stenella* and *Delphinus*, along with the targeted and closely associated yellowfin tuna, *Thunnus albacares*. The National Marine Fisheries Service (NMFS) began placing observers on vessels in 1968 after it was reported that large numbers of dolphins were being incidentally killed in the fishery (Perrin 1970). The Inter-American Tropical Tuna Commission (IATTC) started a similar program in 1979 (Hall 1998). *D. delphis* was the third most frequently killed cetacean in this fishery, after pantropical spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphins (Smith 1979; Hall 1998). In addition to mortality estimates, observers collected biological samples from these animals. Using these

Figure 1. Distribution map of *D. delphis* (Heyning and Perrin 1994). Shaded regions indicate the known distribution; outlined areas (N. Pacific, Irish coast, and the Black Sea) indicate populations whose life histories have been studied comprehensively.



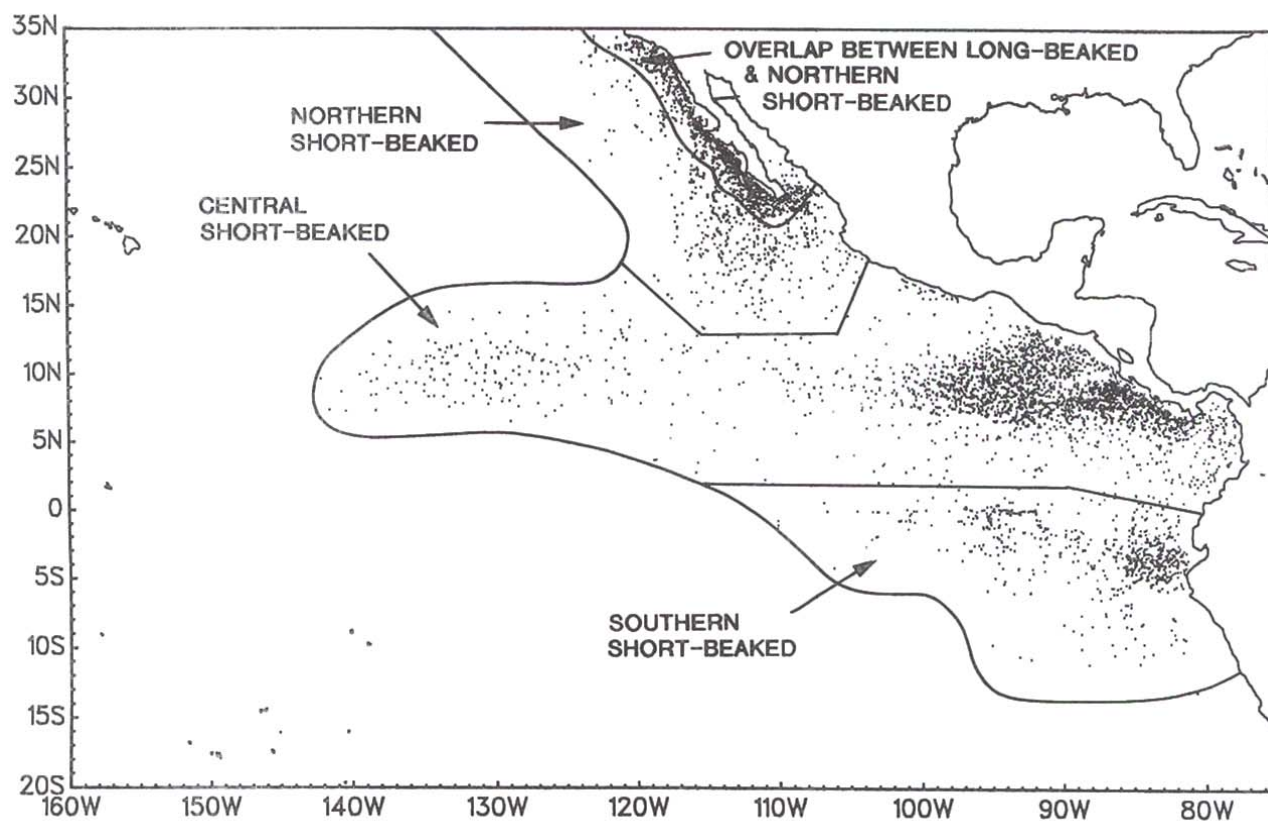
biological samples, extensive life history studies on *S. attenuata* and *S. longirostris* were completed (Perrin et al. 1976a; Perrin et al. 1977). However, prior to this study, a comprehensive life history study of *D. delphis* in the ETP has not been done.

In the ETP, three stocks of *D. delphis* are recognized for management purposes: northern, central, and southern (Figure 2) (Perrin et al. 1985). For marine mammals, the NMFS uses guidelines from the Marine Mammal Protection Act (MMPA) to define the term “stock”. This term refers to “a group of the same species in a common spatial arrangement that interbreed when mature” and “are a significant functioning element in the ecosystem of which they are part of” (Wade and Angliss 1997). For the purposes of this thesis, I use the term “stock” to refer to the management units identified by NMFS under this definition.

The identification of stocks uses the best available data and may include differences in associated parasites (Mattiucci et al. 2004), distribution (Dizon et al. 1994), morphometric and meristic characteristics (Dizon et al. 1994; Turan 2004) genetics (Dizon et al. 1994; Winans et al. 2004) and growth and reproduction (Dizon et al. 1994), or a combination of these factors. *D. delphis* stocks in the ETP were defined by hiatuses in distribution, differences in asymptotic length of adult animals, and differences in breeding seasonality.

Although genetic studies have yet been carried out on these stocks, the described characteristics suggest some degree of reproductive isolation between them (Perrin et al. 1985; Dizon et al. 1994), and thus they are managed separately. Since it is likely that these stocks have different life histories (already reflected in

Figure 2. Distribution and boundaries of *D. delphis* stocks recognized in the eastern tropical Pacific (Dizon et al. 1994).



length and breeding seasonality differences), combining biological samples from all three stocks was not appropriate and I focused on describing the life history characteristics of females from the central stock (which I will refer to as central *D. delphis*), for which the greatest number of samples were available.

This study posed three primary questions: (1) Can age estimations and archiving of tooth slides be improved through the use of an image analysis system? (2) What are the growth and reproductive parameters of central female *D. delphis*? and (3) Does geographic variation occur in female *D. delphis* on both large and fine scales? These three questions are important for management because accuracy of age estimates directly effects reproductive parameter estimates and understanding the basic reproductive parameters and their spatial variation provides essential information to improve management plans for each cetacean species/stock recognized.

These three questions also provide the framework for my thesis, and the results of analyses to address each question are presented in Chapters 3, 4, and 5 respectively. Chapter 2, which follows, presents a review of the literature about all aspects of studying cetacean life history, with emphasis on the literature about small delphinid studies.

CHAPTER 2: LITERATURE REVIEW

Odontocete life history strategy

Life history strategy refers to the parameters that determine growth, reproduction, and survival of an organism. Specific life history strategies vary between and within the suborders of odontocetes, depending on the size, longevity, and environment occupied by the species. In odontocetes, larger and longer-lived animals have slower life history processes than smaller and shorter-lived ones (Boyd et al. 1999; Whitehead and Mann 2000). For example, the relatively small harbor porpoise (*Phocoena phocoena*), which is characterized by a short life span, matures early (at approximately age three) and breeds every one to two years (Read and Hohn 1995). In contrast, the larger and longer-lived killer whale (*Orcinus orca*), matures late (at approximately age 15) and breeds on average every five years (Ford 2001). Longer-lived species can invest more time in their offspring, therefore extending their breeding cycle (Boyd et al. 1999).

Growth varies between the sexes for several cetacean species, leading to some degree of sexual dimorphism. Among some porpoises and the river dolphins (except *Pontoporia blainvillei*), females are slightly larger than males, whereas in the other odontocetes, the reverse is true. Males tend to be 2 to 10% larger than females in the smaller delphinids (Chivers 2002a).

The age at attainment of sexual maturity (ASM) in cetaceans ranges from three to over ten years (Perrin and Reilly 1984), after which they begin giving birth to single, large (40 – 48% of adult female length) precocial young. At least

some seasonality in reproduction has been described for all cetaceans studied in detail (Perrin and Reilly 1984) and a general trend of increased breeding synchrony at temperate latitudes compared to tropical latitudes has been noted (Barlow 1984; Whitehead and Mann 2000; Chivers 2002a). Chivers (2002a) described a typical 2- to 3-year breeding cycle for small delphinids, consisting of an 11- to 12-month gestation, followed by a lactation period of 1-2 years, and then a period of rest preceding the next pregnancy. Parental care is left solely to the mother, although allomaternal care has been described for some species (Wells et al. 2002). Fertility and reproductive success are generally lower in newly mature females; then they peak, plateau, and decrease again with age (Lockyer and Sigurjonsson 1992; Martin and Rothery 1993; Robeck et al. 1994; Boyd et al. 1999).

Age

Interpreting and understanding the biology and population dynamics of cetaceans are aided by examining relationships of reproduction, growth, food habits, and habitat use with age. Age is a fundamental element for describing life history parameters, providing the basis for describing the age structure and longevity of individuals in a population, estimating individual growth rates from birth to adulthood, and estimating age-specific rates of birth and survival. In particular, age specific rates of growth and survival are important for estimating population growth rates and modeling population dynamics.

Age can be estimated by counting growth layers in teeth, similar in concept to reading growth rings in trees. The value of studying annual growth layers in

marine mammal teeth was first noted by Scheffer (1950) in his study of the fur seal (*Callorhinus ursinus*). Since then, growth layers have been studied in many other pinnipeds and several odontocetes (Myrick et al. 1983; Hohn et al. 1989; Stewart et al. 1996).

Tooth morphology

Each delphinid tooth is comprised of the inner dentine, which is covered by a thin layer of enamel on the crown and basally by cementum (Perrin and Myrick 1980). Orban (Orban 1976a, b) described dentine and cementum as composed of organic collagen and polysaccharides and inorganic hydroxyapatite (calcium and phosphate). The ratio of organic to inorganic components differentiates dentine from cementum. Newly formed dentine accumulates on the internal surface, adjacent to the pulp cavity, whereas cementum deposits on the external surface of the root of the tooth (Myrick et al. 1983).

Growth layer groups

Incremental growth in the dentine and cementum of the tooth begins to accumulate after birth, forming regularly spaced lines, termed growth layer groups (GLGs), that usually coincide with an annual rate of accumulation (Perrin and Myrick 1980). A hypocalcified band in the dentine, termed the neonatal line, serves as a baseline for all other lines that are laid down. This line forms at birth in response to abrupt environmental and nutritional changes at that time (Orban 1976a). The cemental layer, which is deposited postnatally, is usually thin, resulting in very fine GLGs compared to those in the dentine. For this reason, age is usually estimated by examining GLGs in the dentine (Hohn 2002).

Several different annual layering patterns have been described for different dolphin species. Myrick et al. (1983) described a GLG pattern in thin stained sectioned teeth of *S. attenuata* and *S. longirostris* as consisting of four components: a thin lightly stained layer, followed by a thick dark stained layer, followed by a second thin lightly stained layer, and another thick dark stained layer. A single layer with a mid-GLG accessory layer has been described for bottlenose dolphin (*Tursiops truncatus*) teeth (Hohn 1980b), while an annual deposition of two layers has been described for beluga whales (*Delphinapterus leucas*). Often, GLG boundaries appear as narrow darkly stained layers (Hohn et al. 1989).

Several methods have been used to calibrate dentinal GLGs with time and to determine their deposition rate in odontocetes. These include tetracycline labeling of teeth, examination of teeth from known-age animals, and multiple extractions and examinations of teeth over time (Gurevich et al. 1980; Hui 1980; Myrick et al. 1984; Hohn et al. 1989; Myrick and Cornell 1990). Using tetracycline-labeled teeth, Gurevich et al. (1980) and Myrick et al. (1984) found that one GLG is laid down annually in *D. delphis* and in *S. longirostris* teeth, respectively. Hohn et al. (1989) used teeth from known-age animals as well as multiple extractions over time to define annual GLGs in *T. truncatus*. In odontocetes, GLG thickness is age specific and decreases with increasing age (Myrick et al. 1984; Hohn et al. 1989; Myrick and Cornell 1990). Hohn et al. (1989) suggested that approximate GLG widths and structures described in their

study of *T. truncatus* could be used as a model for defining layers in other delphinid teeth for which GLGs have not been calibrated.

Marker lines

A series of accessory layers within each GLG correspond to lunar monthly cycles and daily incremental growth (lines of Ebner) in the dentine (Perrin and Myrick 1980). However, accentuated lines caused by interruption in the mineralization process do occur, forming the lines of Owen (Orban 1976a) or “marker lines”. Marker lines have been attributed to calving and maturation events (Klevezal and Myrick 1984; Hohn et al. 1989), as well as to changes in feeding habits associated with environmental events (Manzanilla 1989).

Aging techniques

Several different preparation techniques and viewing platforms have been used for estimating age for small delphinids and porpoises and each has advantages and disadvantages. However, the same technique needs to be used when comparing ages (or parameters calculated using age as a variable) across samples or populations. This is because different age estimation techniques have been shown to create biases in described age-structure of marine mammal populations (Oosthuizen and Bester 1997; Hohn and Fernandez 1999).

Traditional preparation methods

Unstained or decalcified and stained thin sections have been the most commonly used preparations for age determination in small odontocetes. Unstained longitudinal thin sections, which range from 30 μm to 300 μm and are examined by light microscopy, are relatively easy to prepare (Perrin and Donovan 1984; Hohn and Fernandez 1999) but are now thought to produce biased and

potentially inaccurate age estimates (Hohn and Fernandez 1999). Specifically, an underestimate of age for older individuals occurred when using unstained sections. Preparation of stained thin sections is more difficult but allows more accurate estimates of age (Hohn and Fernandez 1999). Teeth are decalcified for several hours, cut with a freezing microtome into 25 μm -thick longitudinal serial sections, and stained with hematoxylin (Myrick et al. 1983).

Scanning electron microscopy

Opinions on the value of using scanning electron microscopy (SEM) for age determination are conflicting. Hohn (1980a) presented preliminary results indicating that SEM permits the best resolution of GLGs in *T. truncatus*, while microradiography best determines the nature and extent of newly forming GLGs. However, Oosthuizen and Bester (1997) found that the accuracy of ages determined from SEM images of GLGs in the dentine of fur seals was poor. This was due to incremental layers being hard to distinguish from GLGs because the relief of finer details was enhanced. Goren et al. (1987) viewed GLGs in cross sections of *D. leucas* teeth with SEM but were unable to estimate age using this method.

Additional techniques

Additional preparation techniques have been employed in the past to examine growth layers in odontocete teeth. Acid etching, which was traditionally used on pinniped teeth, was shown to produce good results with larger toothed cetaceans such *O. orca* and sperm whales (*Physeter macrocephalus*) (Pierce and Kajimura 1980). Polarized light microscopy has been used to delineate

boundaries of GLGs by examining the microstructure of dentine and cementum (Myrick 1980).

Sexual Maturity

Female cetaceans are considered sexually mature when an animal has ovulated at least once (Perrin and Reilly 1984). This is determined by the presence of a *corpus luteum* or one or more *corpora albicantia* on the ovaries. The *corpus luteum* is an endocrine gland, which develops from the ovarian follicle after ovulation, either regressing if fertilization does not occur or persisting throughout pregnancy, secreting necessary hormones. A regressed or regressing *corpus luteum* is termed a *corpus albicans* (Perrin and Donovan 1984). *Corpora atretica* are fibrous bodies on the ovary that form as a result of follicular degeneration not associated with ovulation (Akin et al. 1993).

Females become sexually mature at approximately 85% of their asymptotic length (Laws 1956), at which point primary allocation of resources is directed towards reproduction rather than growth (Chivers 2002a). The average ASM occurs over a fairly wide range of ages in toothed cetaceans: 3 - 10 years (Perrin and Reilly 1984), although there is a greater range of ages over which individual animals reach sexual maturity. In the ETP, ASM ranges from 7 to 16 years of age in *S. attenuata* (Myrick et al. 1986; Chivers and Myrick 1993) and from 5 to 12 years of age in *S. longirostris* (Perrin et al. 1977). Calculating the average ASM for a population allows the average reproductive potential of females in a population to be estimated. The average ASM for a population may change in response to variations in population density, food supply, and environmental

conditions (Lockyer 1984; Fowler 1987; Lockyer 1990). That is, a decrease in the average ASM is predicted to occur when population abundance declines (Eberhardt and Siniff 1977; Reznick and Bryga 1990). The average ASM as well as the range of ASM for individuals also differs between species and may be due to (Marsh and Kasuya 1984) differences in growth rates (Whitehead and Mann 2000).

After reaching sexual maturity, survivorship remains high during the reproductive years and small delphinids typically produce a calf every three to four years (Chivers 2002a). The occurrence of post-reproductive females has been reported in a few odontocete species: short-finned pilot whales (*Globicephala macrorhynchus*), *S. attenuata*, and *O. orca* (Marsh and Kasuya 1984; Myrick et al. 1986; Olesiuk et al. 1990), and likely contributes to increased reproductive success of a population if post-reproductive females care for the young of other females (Boyd et al. 1999). However, post-reproductive females are rare among cetacean species.

Variation in Cetacean Reproduction

Spatial and temporal

Reproductive seasonality has been documented for all delphinids studied in detail. However, the intensity of breeding peaks varies between species and their geographic locations (Perrin and Reilly 1984). In general, breeding is highly synchronous in temperate latitudes and tends to be more diffuse in tropical latitudes (Barlow 1984; Whitehead and Mann 2000; Chivers 2002a). For example, all births occur within a few weeks in *P. phocoena* (Read 1990), which breeds in northern temperate waters, while the tropical *Stenella* spp. give birth

throughout the year with broad seasonal peaks (Barlow 1984). However, localized differences in timing of reproduction have been noted in neighboring *T. truncatus* populations, which are the most studied of the small delphinid species. Along the coast of Texas, *T. truncatus* breeds two months earlier than the population along the west coast of Florida, and Urian et al. (1996) suggested that the differences in timing of the breeding seasons for *T. truncatus* populations in warm-temperate waters are the result of localized adaptations. They hypothesize that seasonal changes in prey distribution affect the timing of reproduction so that prey availability is maximized during periods of high-energy demand for mothers and offspring.

The average ASM has been documented to vary between populations of marine mammals (Chivers and Myrick 1993) as well as with changes in prey resources (Lockyer 1990) and population size (Kasuya 1985). Specifically, a decrease in average ASM has been correlated with increased food availability in crabeater seals (*Lobodon carcinophaga*) (Bengtson and Laws 1985) and Icelandic fin whales (*Balaenoptera physalus*) (Lockyer 1990). Changes in growth rates, which likely result in a change in average ASM, have also been linked to changes in food availability and environmental conditions in southern hemisphere baleen whales (Lockyer 1990).

Variation in length at attainment of sexual maturity (LSM) has been noted in both dolphins and baleen whales. The response of this parameter is poorly understood but several hypotheses have been proposed. A temporal change in the average LSM, without a corresponding change in the average ASM, was found in

ETP *S. attenuata* and was thought to reflect a change in growth rate (Barlow 1985). The small sample size of aged individuals was suggested by Barlow (1985) as the reason that a significant change in ASM could not be detected. Lockyer (1990) observed that increased individual growth rates correlated with earlier ASM in *B. physalus*, but there was no corresponding change in LSM detected. These differences in LSM patterns between studies may simply reflect flexibility in the parameter and adaptations to local environments or perhaps even biases in recorded length measurements. LSM has also been found to differ between populations of cetaceans. For example, Best (2001) observed differences in LSM in a comparison of inshore and offshore populations of Bryde's whales (*Balaenoptera edeni*) off South Africa, leading him to hypothesize that they were reproductively isolated.

Density dependence

Changes in mortality, growth, maturity, or reproduction may occur in response to changes in population size or density (Fowler 1987). For large mammals, density-dependent changes are predicted to occur in populations close to their carrying capacities (Fowler 1981). Density-dependent responses are triggered by changes in the per-capita availability of limiting resources, which are typically food availability related to changes in environmental conditions or population abundance. Eberhardt and Siniff (1977) and Eberhardt (1977) hypothesized an order of expected compensatory responses for large long-lived mammals, starting with changes in juvenile survival rates, followed by changes in the average ASM and reproductive rates, and finally adult survival. For example, if populations are below carrying capacity, per-capita resources are more

plentiful, and the overall condition of individuals improves, which improves the animals' ability to survive and for females to more successfully produce viable young.

Density-dependent responses can be observed in response to fishery pressure, if the fishery kills animals in sufficient numbers to effectively increase per-capita resource availability. Perrin et al. (1976a) found differences in life history parameters between two populations of *S. attenuata* exposed to different levels of exploitation. In the more exploited population in the ETP, pregnancy rates were higher and birthing intervals were shorter compared to the less exploited Japanese population. Perrin et al. (1977) have also suggested that differences in reproductive rates between *S. attenuata* and *S. longirostris* in the ETP are related to differential exploitation. However, Perrin and Henderson (1984) did not observe expected differences between two populations of *S. longirostris* in the ETP with different histories of exploitation leaving the interpretation open as to whether exploitation or inherent population differences resulted in the different reproductive rates for eastern and western Pacific populations.

Lockyer (1990) suggested that temporal variation in the average ASM and growth rates of Icelandic fin whales was a density-dependent response to changes in prey abundance. A decrease in the average ASM was observed during a period for which an increase in krill in the Antarctic is thought to have resulted from decreased predation by baleen whales due to whaling. An increase in average ASM was then observed to be associated with a decline in zooplankton abundance

associated with a sudden drop in salinity and sea surface temperature from the mid 1960s until the mid 1980s.

***Delphinus delphis* Overview**

Taxonomic relationships

Two species of *Delphinus* are currently recognized: the short-beaked *D. delphis* and the long-beaked *D. capensis*. These species designations were based on morphometric analyses of total body and rostral lengths, as well as differences in color patterns (Heyning and Perrin 1994). These designations are also supported by molecular genetic differences between the two forms (Rosel et al. 1994). In the North Pacific, before *D. delphis* and *D. capensis* were officially designated as being distinct species, they were recognized as different forms and were referred to as “offshore” and “neritic” or “Baja-neritic”, respectively. Off California, *D. capensis* was once considered to be *D. bairdii*, and is so referred to in the older literature. Recently, the taxonomic status of a third morphotype was described from the Indo-Pacific Oceans and has been designated a subspecies: *D. capensis tropicalis* (Jefferson and Van Waerebeek 2002).

Abundance and distribution

In the eastern Pacific, *D. delphis* range from British Columbia to Chile and from their coasts to 135° W. Sightings have been recorded in the central Pacific north of Hawaii and in the western Pacific off New Caledonia, New Zealand, and Japan. In the western Atlantic, records range from Newfoundland south to Florida and in the eastern Atlantic from northern Europe to the west coast of Africa. *D. delphis* is also found in the Black and Mediterranean Seas (Heyning and Perrin 1994).

Within these ocean basins, sightings of *D. delphis* have been correlated with sea surface temperature (SST), thermocline, salinity, and bathymetry. *D. delphis* are typically associated with water masses having SSTs less than 28 °C in the northeastern Pacific (Evans 1982) and between 5.0 and 22.5 °C in the Atlantic (Selzer and Payne 1988). Surface salinity values at sighting locations in the Atlantic ranged from 32 to 35 ppt (Selzer and Payne 1988). Sightings of *D. delphis* have been more frequent in areas of high relief, such as escarpments or seamounts, in both the Pacific and the Atlantic Oceans (Hui 1979b; Selzer and Payne 1988). The correlation with environmental features appears to be the result of upwelling that provide greater feeding opportunities for *D. delphis* (Hui 1979b; Selzer and Payne 1988). *D. delphis* distribution in the ETP was also found to be associated with upwelling areas linked with cool SSTs and weak shallow thermoclines (Au and Perryman 1985; Reilly 1990). Seasonal north/south and inshore/offshore movements have been described for *Delphinus* spp. off California and are thought to occur in response to changing oceanographic conditions (Forney and Barlow 1998). During the winter, the population of *D. delphis* off California moves closer to shore and is distributed farther south than in the summer. Similarly, a seasonal offshore shift in *D. delphis* distribution also occurs in New Zealand, with distance from shore decreasing during periods of warmer SST (Neumann 2001).

A decrease in the abundance of the northern stock of *D. delphis* in the ETP and a concomitant increase off southern California, starting in the late 1970s, suggests that a large-scale shift in the distribution of *D. delphis* occurred in the

eastern North Pacific (Anganuzzi and Buckland 1994). However, incidental mortalities in the tuna fishery are thought to be the cause of the decline of the central stock of *D. delphis* from 1976 to the early 1980s, when the stock was reduced from approximately 400,000 to 200,000 individuals. By the mid 1980s, the population began slowly increasing and is now thought to be stable (Anganuzzi and Buckland 1994).

Life History of *Delphinus delphis*

Life history characteristics have been observed to differ among geographic regions (Table 1). The North Pacific is defined here as the region of the Pacific Ocean north of the equator. Data from the central North Pacific encompass the region from 45° N to 29° N and from 147° E to 150° W. The eastern tropical Pacific is defined as the area east of 180° W and between 30° N and 20° S.

Central North Pacific

In the North Pacific Ocean, Ferrero and Walker (1994) estimated that *D. delphis* females reach sexual maturity at between 7.2 and 8.5 years, at a length of 172.8 cm or 170.7 cm based on the DeMaster and logistic methods respectively (DeMaster 1978; Cox and Snell 1989). Mean length of adult females was 179.8 cm. Gestation was estimated to be 11.1 months based on a length-at-birth estimate from a single neonate of 82.0 cm. A mid-May or early June seasonal peak in calving was noted. In addition to small numbers of neonates and pregnant females in the sample, age and length distributions suggested that herd composition varies spatially in this area. The maximum reported age was 26 years for females and 27 years for males.

Table 1. Regional life history characteristics of female *D. delphis*.

An asterisk indicates studies that defined sub-regions differently than what is used presently. ELB = estimated length at birth, ASM = age at sexual maturity, LSM = length at sexual maturity, APR = annual pregnancy rate.

Region	Mean Adult Female Length (cm)		ELB (cm)	ASM (years)	LSM (cm)	Gestation (months)	Lactation (months)	Resting (months)	Calving interval (years) (1/APR)/Sum of Phases	Calving peak
Central North Pacific (Ferrero and Walker 1994)	179.8		82.0	7.2-8.5	170.7 or 172.8	11.1				May-June
Eastern North Pacific (Harrison et al. 1969) (Evans 1975) (Hui 1979a)			75-90	7-14	165-182					Dec-March Spring/Fall
Eastern Tropical Pacific Northern Central Southern	(Perryman and Lynn 1993) 179.2 194.8 184.3	(Perrin et al. 1985) 178.5 194.3	(Hui 1977)* 81.3 79.0			(Henderson et al. 1980)* 11.5 11.5 11.5	(Henderson et al. 1980)* 24.2 19.3	(Henderson et al. 1980)* 1.2 3.7	(Henderson et al. 1980)* 2.88/3.07 2.56/2.88	(Perryman and Lynn 1993) January-July None Jan-June

Region	Mean Adult Female Length (cm)	ELB (cm)	ASM (years)	LSM (cm)	Gestation (months)	Lactation (months)	Resting (months)	Calving interval (years) (1/APR)/Sum of Phases	Calving Peak
Black Sea (Kleinenberg 1956) (Tomlin 1957)		82-90 85	3						May-September June-August
N.E. Atlantic (Murphy 2004)		104.1	9-10		11.5	10.35	20.7	3.55	May-September

Eastern North Pacific

A mid-to late-summer breeding peak has been suggested for *D. delphis bairdii* off California (Ridgway and Green 1967). However, this was based on temporal variation in testis size from only three individuals, which are now thought to be *D. capensis* (Heyning and Perrin 1994), and thus is not comparable to *D. delphis*. Harrison et al. (1972) found evidence of testicular enlargement and activity throughout the year with peaks in spring and summer in *Delphinus* spp. off California, thus suggesting diffuse breeding peaks that may actually represent the two *Delphinus* spp. or perhaps different populations.

In southern California waters, Hui (1979a) reported *Delphinus* spp. females reaching sexual maturity between 7-14 GLGs and 175-190 cm. Gaps in the occurrence of specimens just prior to sexual maturation (4-8 GLGs) suggest possible segregation of individuals according to maturity status in this population (Hui 1979a). Harrison et al. (1972) suggested that calving occurs from December to March. However, it is not known whether sampled individuals from these studies were *D. delphis* and/or *D. capensis*. Using neonatal and fetal length distributed by month, Evans (1975) suggested a bimodal calving season in spring and fall for the southern California population of *D. delphis*.

Eastern Tropical Pacific

Using data from 1973 to 1978, Henderson et al. (1980) summarized reproductive parameters for female *D. delphis* of the central tropical stock. This study used stock boundaries that were slightly differently from those currently used (Perrin et al. 1985). In that study, 47.7% of females were reproductively mature and were estimated to have a lactation period of 19.3 months, a 0.390

annual pregnancy rate (APR), and a calving interval of 2.88 years (sum of phases) or 2.56 years (1/APR).

Perryman and Lynn (1993) obtained total body length data from aerial photographs, which revealed that the mean length of adult females and the timing of reproduction differ among the three ETP stocks of *D. delphis*. Mean length of adult females was 179.2 cm, 194.8 cm, and 184.3 cm for the northern, central, and southern stocks, respectively. A pulse in reproduction from January through July was found in the northern stock, no seasonality in the central stock, and strong seasonality in the southern stock with all births occurring during the first six months of the year.

Black Sea

Length of female *D. delphis* in the Black Sea ranges from 80 to 194 cm, with an average of 158.7 cm (Tomlin 1957). Sexual maturity in females was attained between 161-200 cm in total length and three years of age (Kleinenberg 1956). However, the methods used for age determination for the Black Sea animals were unclear. Collet and St. Girons (1984) questioned the accuracy of the average ASM estimates of the Black Sea animals because it was so different from more recent estimates of other *D. delphis* populations. Kleinenberg (1956) and Tomlin (1957) documented herd segregation according to reproductive condition of *D. delphis* in the Black Sea. Females predominantly occur offshore during periods of calving and early lactation. A single calving season, which coincides with warm SSTs (Evans 1975), occurs from June to August (Tomlin 1957).

Northeast Atlantic

In the N.E. Atlantic, Murphy (2004) found that females ranged from 93 to 216 cm in total length and attained sexual maturity between 9 and 10 years of age. A calving interval of 42.5 months was determined by summing the calculated gestation period of 11.5 months, the lactation period of 10.35 months, and the resting period of 20.7 months. Reproduction was seasonal, with calving and the male breeding period occurring from May to September. *Corpora* scars did not accumulate with age, which the author attributed to possible resorption of ovarian scars with age and to individual variation. Evidence of senescent females was not found.

ETP Central Stock *D. delphis* Habitat

Overview

The overall area within the central stock boundaries is characterized by warm, low-salinity waters, a strong shallow thermocline, and a thick oxygen minimum layer just below the thermocline (Wyrcki 1966). However, concentrations of *D. delphis* are found in upwelling modified regions in this area, with cool surface temperature and a shallow, weak thermocline (Au and Perryman 1985; Fiedler and Reilly 1994). This type of habitat is found in the equatorial and eastern boundary current (California and Peru Currents) systems of the ETP and seasonally around the Costa Rica Dome (Fiedler and Reilly 1994).

Topography

Wyrcki (1966) noted that depths in this region range from 3500 to 4500 m, with the exception of the Acapulco Trench, which exceeds 6200 m near 14° N, 94° W. The continental shelf is narrow, with a steep continental slope. However,

the shelf is greater than 50 km wide between the Gulf of Tehuantepec and Nicaragua, as well as in the Gulf of Panama. The East Pacific Rise stretches north to south, surrounded by a number of seamounts and islands, while the Cocos Ridge stretches southwest from Central America (Wyrski 1966). Topography of the area is important because *D. delphis* distribution has been correlated with bottom topography (Evans 1975; Hui 1979b; Selzer and Payne 1988).

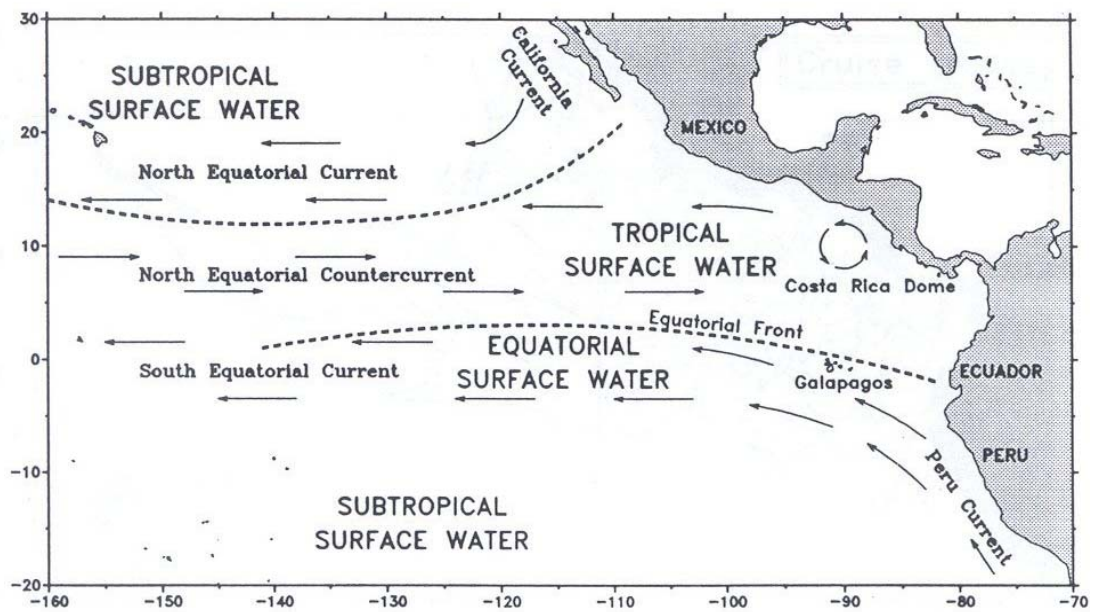
Circulation

The southward California Current and the northward Peru Current feed into the westward North and South Equatorial Currents (NEC, SEC). Between the NEC and SEC, the North Equatorial Countercurrent (NECC) flows eastward (Figure 3). From September through December the NECC is strong, but it becomes weak or absent from February through April (Fiedler and Reilly 1994). A cyclonic eddy, the Costa Rica Dome, encompasses an area of approximately 200 to 400 km in diameter (Hofmann et al. 1981) and is centered at approximately 9° N, 89° W, at the eastern edge of a thermocline ridge. This eddy is known to fluctuate $\pm 1^\circ$ of latitude and longitude (Wyrski 1964).

Upwelling

Equatorward longshore winds off Peru and Baja California, in addition to trade winds along the equator, drive upwelling in the ETP by bringing sub-thermocline cold, nutrient-rich water to the surface (Reilly and Fiedler 1994). This results in high levels of new production in equatorial and eastern boundary current systems by providing optimal levels of nitrogen to phytoplankton at the surface (Chavez and Barber 1987). A seasonal pattern of a spring minimum and a

Figure 3. Surface circulation and water masses of the eastern tropical Pacific
(Reilly and Fiedler 1994).



fall maximum for phytoplankton pigment concentrations has been observed for equatorial surface waters as well as those between the NEC and NECC (except the Costa Rica Dome) (Fiedler 1994).

Upwelling also results from intermittent, topographically induced offshore winds along several points off Central America, including the Gulfs of Tehuantepec, Papagayo, and Panama. These winds are generally strongest during the winter (McCreary et al. 1989) and are followed by seasonal peaks in phytoplankton pigment concentration (Fiedler 1994). In addition, upwelling occurs in the region of the Costa Rica Dome (Figure 3) due to doming of isotherms caused either by cyclonic circulation created by the NECC and the NEC (Wyrtki 1964) and/or by cyclonic wind stress curl (Hofmann et al. 1981). In conjunction with the northward movement of the intertropical convergence zone (ITCZ), cyclonic wind stress intensifies during the late spring and early summer in the region of the Costa Rica Dome, producing localized upwelling throughout summer and early fall (Hofmann et al. 1981; Fiedler 1994). The upwelled region is released as a Rossby wave in November and propagates to the west (Hofmann et al. 1981).

Seasonal and interannual variability in habitat

Au and Perryman (1985) first hypothesized that the distribution of *D. delphis* in the ETP was correlated to cool, saline “upwelling modified” waters. Fiedler and Reilly (1994) defined habitat quality for three species of dolphins in the ETP by correlating species abundance with environmental conditions (SST, thermocline depth, and thermocline thickness). *D. delphis* habitat was

characterized by cool surface temperature and a shallow, weak thermocline, indicative of upwelling.

Fiedler and Reilly (1994) presented a time series of habitat quality for *D. delphis*, *S. longirostris*, *S. attenuata*, and striped (*S. coeruleoalba*) dolphins in the ETP from 1975 to 1990. For all species, a strong interannual signal was attributed to the El Niño events of 1982-83 and 1986-87. The habitat quality for *D. delphis* decreased during those time periods. In early 1983, little favorable habitat was available to *D. delphis* in the ETP, except in equatorial waters west of the Galapagos. However, in early 1985 favorable habitat expanded for the central and southern stocks along 10° N and the equator, respectively. Seasonal variability in habitat quality for *D. delphis* was relatively low when compared to that of the *S. l. orientalis* and *S. attenuata*. However, habitat quality appeared to be highest from December through February and lowest from June through August. Reilly (1990) did not observe major seasonal shifts in the distribution of *D. delphis* but found year-round density-centers of *D. delphis* that occurred in upwelling modified habitats near the Revillagigedos Islands, along the coasts of Baja California and Ecuador, and near the Costa Rica Dome.

Dolphin mortality in the ETP purse-seine fishery

During the 1960s, total dolphin mortality caused by the tuna purse-seine fishery was estimated to be hundreds of thousands of animals per year (Smith 1983). Most populations declined until the late 1970s and leveled off in the early to mid 1980s due to the implementation of methods and devices mandated by regulations to reduce mortality (Hall 1998). Incidental dolphin mortality had been

reduced to approximately 3600 by 1993 (Lennert and Hall 1995), and has been below 2000 since 1998 (Bayliff 2002). Specifically, for the years 1979 through 2002, central *D. delphis* mortality peaked at 12,711 animals in 1989 and was reduced to 230 by 1993. Central *D. delphis* mortality has fluctuated between 34 and 222 animals between 1994 and 2002 (Bayliff 2002).

Collection of biological data from central *D. delphis* incidentally killed in the tuna purse-seine fishery began in 1971. Only adult females were selected for sampling from 1971 through September 1972, after which no selection criteria were imposed and observers collecting data were instructed to sample the first animals brought on board (Perrin et al. 1976a).

Summary

Considerable work has been done over the years to explore aging of delphinid teeth, from calibration of GLGs to investigating tooth preparation techniques. Recently, technological advances have made digital imaging a potential tool in this field. However, no quantitative data are currently available to assess the viability of digital imaging as an aging platform. Thus, the next chapter, Chapter 3, explores whether enhanced digital microscopy is a viable alternative to traditional microscopy for aging delphinid teeth.

In the Pacific Ocean, the most comprehensive life history study of *D. delphis* to date has been on the central north Pacific population. The only information available on currently managed stocks of *D. delphis* in the ETP describes seasonality in reproduction and mean length of adult females. A large gap in our understanding of this species in this region of the Pacific has remained

until now. Chapter 4 presents the first comprehensive study of growth and reproduction of *D. delphis* in the ETP. These data can be used as a comparison with other populations and as a basis for modeling population dynamics and improving management of this species.

The oceanography of the region and habitat preferences of *D. delphis* has been well documented over the years. However, the potential interplay of habitat and life history has never been directly investigated in the ETP for any of the pelagic dolphins inhabiting the area. Thus, Chapter 5 is devoted to analyses conducted to determine whether habitat influences fine scale geographic variation in life history parameters and potentially population structure.

CHAPTER 3: PRECISION AND BIAS OF AGE DETERMINATIONS USING LIGHT MICROSCOPY AND ENHANCED DIGITAL MICROSCOPY.

Introduction

Age is a fundamental parameter for describing the life history of a species. It provides the basis for quantifying the reproductive potential of a population and estimating individual growth rates from birth to adulthood and schedules of birth and survival. Thus, it is essential that the method of estimating this parameter maximize precision and accuracy in order to obtain the best age estimate possible. This study explores the use of a new method which has proven successful in aging fish otoliths (Neal 1987; Laidig and Pearson 1992; Caillet et al. 1996) and examines its associated precision and biases in aging *D. delphis* teeth.

Age has been estimated in many species of delphinids by examining growth layers in the teeth. Incremental growth in the dentine and cementum of the tooth begins after birth and accumulated layers defined by regularly spaced major lines are referred to as growth layer groups (GLGs). In small delphinids, the concept that GLGs correspond to an annual rate of accumulation (Perrin and Myrick 1980) is generally accepted and supported by several calibration studies (Gurevich et al. 1980; Myrick et al. 1984; Hohn et al. 1989; Myrick and Cornell 1990). Using tetracycline labeled teeth, Gurevich et al. (1980) determined that one GLG is laid down annually in the teeth of *D. delphis*, and so in this study each GLG is equated with one year of life.

Traditionally, age estimates are obtained in delphinids by counting GLGs in stained thin sections of teeth mounted on slides and viewed through a

compound light microscope. However, stained thin sections run the risk of fading with time. This has occurred in the past (K.M. Robertson, personal communication) and been remedied with alternative sealing media (Lockyer 1995). However, it is currently not known how long current stains will last, and a method for archiving prepared tooth sections is needed so that teeth may be referenced far into the future. In addition to this need, the prospect of improving the clarity of GLGs (and therefore precision and accuracy) and saving reader GLG designations with their associated teeth led to the exploration of using enhanced digital images obtained from the microscope for estimating ages. Digital imaging equipment has been used to measure widths of incomplete GLGs in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Ferrero and Walker 1996) but not as a platform to estimate age from prepared tooth sections of marine mammal teeth.

In order to determine whether this method might be a viable alternative to traditional microscopy, this study focused on whether (a) precision in age estimations could be maintained or improved on the image analyzer, (b) age estimates or biases differed between viewing platforms, and (c) discrepancies in age differences between readers could be explained by saved GLG demarcations. Teeth from *D. delphis* incidentally caught in gillnets of California (Chivers et al. 1997) were used to investigate these questions.

Methods

Preparation and Age Determination

Teeth were obtained from 36 *D. delphis* incidentally killed in the California gillnet fishery between 1994 and 1997 (Chivers et al. 1997). Following

the protocol of Myrick et al. (1983), teeth were decalcified, cut with a freezing microtome into 25 μ m thick longitudinal serial sections, and stained with hematoxylin. Decalcification times ranged from one to 16 hours, with longer times needed for larger, older animals that had accumulated more dentine and cementum. Sections were mounted on gelatin-coated slides, and cover slip margins were sealed with DPX mounting medium (Lockyer 1995). Ages were determined by counting GLGs in the dentine (Myrick et al. 1983; Hohn et al. 1989), using both a compound light microscope and enhanced video microscope images. Two readers aged each tooth three times, with at least a week between readings, on each viewing platform. GLG estimates were made without reference to specimen information, such as total body length, reproductive status, or previous GLG counts. The mean GLG count of a reader's three age estimations was used to compare precision and ages between readers. The mean GLG count of both readers' three readings is referred to as the total pooled mean age estimate for each specimen.

Video microscope images

Tooth images were captured using the precision megapixel digital camera DVC-1310C and then viewed and enhanced using Image Pro-Plus software (version 4.5). Multiple partial images of each tooth, viewed with the 100x objective, were captured and spliced together to produce a single image of the entire tooth. In older animals, it was often necessary to save an additional image centered on the pulp cavity at 400x magnification. All images were enhanced by increasing brightness and contrast and applying sharpen and Hi Gauss filters to maximize the resolution of GLGs. To maintain consistency, both readers viewed

the same enhanced image. During each aging session, the boundaries of each GLG were marked and the corresponding width measurement of each GLG was saved with the specimen's age file. These marked GLG boundaries were not viewed during subsequent aging sessions.

Intra-Reader Variation

For each reader and viewing platform, the coefficient of variation ($CV = \frac{SD}{\bar{X}} \times 100$) and an index of precision ($D = CV/\sqrt{n}$) was calculated for each tooth, and the mean of these values were used for comparisons (Chang 1982). Because these measures of precision are effectively the same (demonstrated the same trends), D was reported only for comparison to other studies and CV was used in analyses of reader precision and bias. To determine whether precision varied with increasing GLGs, a Spearman rank correlation test was conducted on CV and GLGs.

Inter-Reader Variation

In addition to t -tests and analyses of variance (ANOVA), CV s, age-frequency tables, and age-bias plots were used to compare matched pairs of GLG determinations. Campana et al. (1995) suggested these additional comparison methods as a way of detecting non-linear biases (i.e., biases correlated with age), which t -tests and ANOVA generally cannot detect. The mean ages reported by the two readers were compared for each viewing platform using a paired t -test. Due to heteroscedascity in CV data, the non-parametric alternative to the two-way ANOVA, the Scheirer-Ray-Hare test (Sokal and Rohlf 1995), was used to compare CV across readers for two GLG groups. The GLG groups were based on

a departure of paired age estimations from the 1:1 line at approximately ten GLGs in age-bias plots. This observation and its associated implications will be discussed further in following sections. The following GLG groupings were used in this and subsequent analyses: (a) 0 – 9 GLGs (“young animals”) and (b) 10 or more GLGs (“older” animals).

Viewing-Platform Variation

For each reader, a paired *t*-test was used to compare CV between viewing platforms, age-bias plots were used to visually compare ages between viewing platforms, and a one-way ANOVA was used to compare differences in GLG counts between viewing platforms across GLG groups. For each specimen, assignment to GLG group was based on the total pooled mean age estimate.

Results

Microscope

Intra-reader variation

The mean CV and D for Reader 1 were 11.70 % and 6.75 %, respectively. For Reader 2, mean CV was 11.53 % and D was 6.66 %. A Spearman rank correlation test for each reader indicates that there is no relationship between CV and number of GLGs (Table 2).

Inter-reader variation

On the microscope, GLG counts for Reader 1 ranged from 0 to 24 and from 0 to 23 for Reader 2 (Table 3). Mean age estimates for each specimen were not significantly different between readers (*t*-test: $t_{35} = -0.109$, $P = 0.914$). However, the age-bias plot illustrates a subtle bias between readers (Figure 4a). Compared to Reader 1, a small negative bias for GLG counts by Reader 2 is

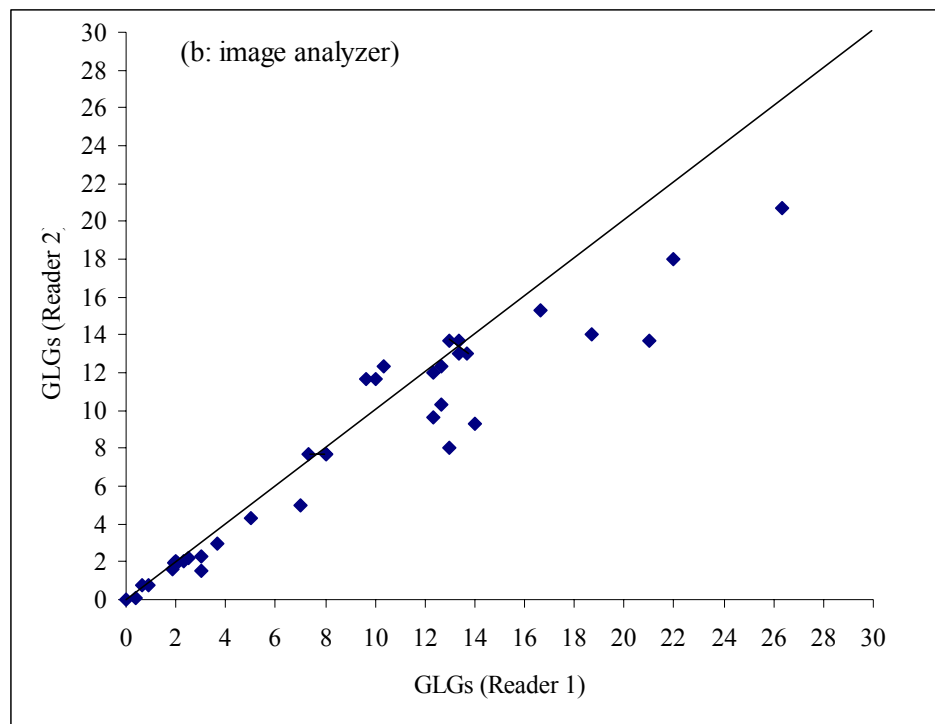
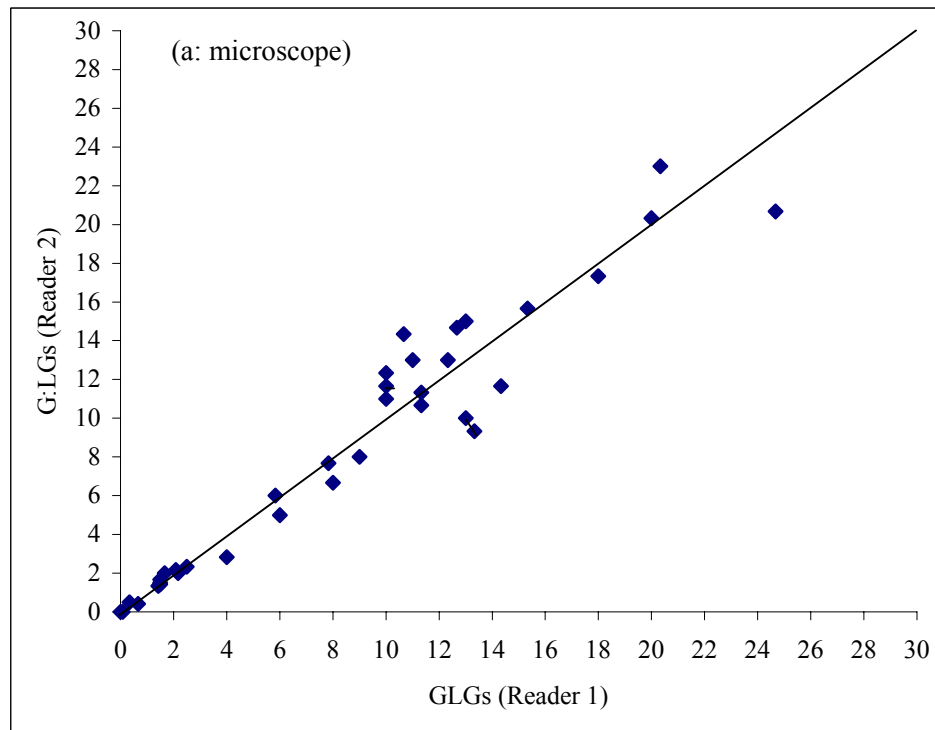
Table 2. Results of Spearman rank correlation test of CV and GLG counts.

	r	P-value
Reader 1		
Microscope	-0.321	0.057
Image Analyzer	-0.053	0.759
Reader 2		
Microscope	0.033	0.850
Image Analyzer	0.060	0.728

Table 3. Frequency of age estimates in GLGs made by Reader 1 and Reader 2 using the microscope. Gray cells illustrate where frequency of age estimates would be located if there were complete concordance in age estimates between readers.

		Ages estimated by reader 2																										
Ages estimated by reader 1		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Total	
	0	4																									4	
	1		4	1																							5	
	2			3																							3	
	3																										0	
	4			1																							1	
	5								1																		1	
	6							1																			1	
	7									1																	1	
	8							1																			1	
	9										1																1	
	10													2	1		1										4	
	11											1		1		1											3	
	12															1	1										2	
	13										1	1						1									3	
	14													1													1	
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	19																										0	
	20																						1			1	2	
	21																										0	
	22																										0	
	23																										0	
	24																						1				1	
	Total	4	4	5	0	0	1	2	1	1	1	2	4	1	2	2	2	0	1	0	0	2	0	0	1	0	36	

Figure 4. Age-bias plots for Reader 1 and Reader 2 by viewing platforms: (a) microscope and (b) image analyzer. The 1:1 line is included for reference to illustrate how the plot would look if there were complete concordance in age estimates between readers.



present from GLGs four to eight, whereas the bias becomes mostly positive from GLGs 10 to 13, and is absent thereafter (although in the last step the sample size was too small to support any conclusions). For specimens where GLG estimations did not agree, 43% agreed to within one GLG and 71% agreed to within two GLGs. Mean CV was not significantly different across readers or age groups ($0.25 < P < 0.50$). Table 4 presents the Scheirer-Ray-Hare summary. Pooling the ages from both readers resulted in a mean CV of 21.3 %.

Image Analyzer

Intra-reader variation

Mean CV and D for Reader 1 were 9.00 % and 5.20 %, respectively. For Reader 2, mean CV was 14.37 % and D was 8.30 %. Spearman rank correlation tests for each reader indicate that there is no relationship between CV and number of GLGs (Table 2).

Inter-reader variation

On the image analyzer, mean GLG counts ranged from 0 to 26 for Reader 1 and from 0 to 20 for Reader 2 (Table 5). Mean GLG estimates were found to be significantly different between readers (t-test: $t_{35} = 3.11$, $P = 0.004$). For specimens where GLG estimations did not agree, 37% agreed to within one GLG and 63% agreed to within two GLGs. Age-bias plots indicate that compared to Reader 1, GLG counts by Reader 2 were negatively biased between three and eight GLGs, positively biased between nine and ten, and negatively biased thereafter (Figure 4b). Mean CV was not significantly different between readers or age groups ($0.90 < P < 0.95$). Table 6 presents the Scheirer-Ray-Hare summary. Pooling the data from both readers resulted in a mean CV of 16.2 %.

Table 4. Scheirer-Ray-Hare summary for microscope, comparing CV across readers and age groups (0-9, 10+).

Source	Sum-of-squares	df	H	P
Reader	2.512	1	0.001	0.975
GLG Group	979.548	1	0.539	$0.25 < P < 0.50$
Reader*GLG Group	2345.058	1	1.291	$0.25 < P < 0.50$
Error	125628.194	68		

Table 5. Frequency of age estimates in GLGs made by Reader 1 and Reader 2 using the image analyzer. Gray cells illustrate where frequency of age estimates would be located if there were complete concordance in age estimates between readers.

		Ages estimated by reader 2																											
Ages estimated by reader 1		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	Total
	0	4																											4
	1		2																										2
	2		1	3																									4
	3		1	1	1																								3
	4																												0
	5					1																							1
	6																												0
	7																												2
	8																												2
	9																												1
	10																												2
	11																												0
	12																												4
	13																												5
	14																												1
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	22																												1
	23																												0
	24																												0
	25																												0
	26																												1
Total		4	4	4	1	1	1	0	3	1	2	1	2	3	5	1	1	0	0	1	0	1	0	0	0	0	0	0	36

Viewing platform comparison

Mean CVs were not significantly different for Reader 1 (t -test: $t_{35} = -1.33$, $P = 0.193$) or Reader 2 (t -test: $t_{35} = 0.548$, $P = 0.587$) on the image analyzer compared to the microscope. Age-bias plots (Figure 5) indicated a departure in GLG comparability between viewing platforms, for Reader 2, at approximately ten GLGs. For specimens with ten GLGs or more, GLG counts by Reader 1 were not significantly different (ANOVA: $F_{1,34} = 3.277$, $P = 0.079$), whereas Reader 2 counted fewer on the image analyzer compared to the microscope (ANOVA: $F_{1,34} = 5.256$, $P = 0.028$). Table 7 presents the ANOVA summary tables for both readers.

Age-bias plots illustrate differences in reader behavior on the two viewing platforms (Figure 4). Biases in GLG counts between readers exhibited the same trend for both viewing platforms until approximately ten GLGs. Up to this point, Reader 2 GLG counts were comparable to those of Reader 1 from zero to two GLGs, negatively biased from approximately three GLGs to eight GLGs, and then became positively biased. However, for age estimations greater than ten GLGs, Reader 2 was negatively biased on the image analyzer and positively biased on the microscope from 10 to 13 GLGs, compared to Reader 1.

Discussion

Although no significant difference in CV across platforms was observed, it is important to note that the readers exhibited opposite trends in precision between platforms. Reader 1 had higher precision (lower CV and D) when using the image analyzer, whereas Reader 2 had higher precision when using the

Table 6. Scheirer-Ray-Hare summary for Image Analyzer, comparing CV between readers and age groups (0-9, 10+).

Source	Sum-of-squares	df	H	P
Reader	525.420	1	0.328	$0.50 < P < 0.75$
GLG Group	2744.170	1	1.713	$0.10 < P < 0.25$
Reader*GLG Group	7.670	1	0.005	$0.90 < P < 0.95$
Error	110448.486	68		

Figure 5. Age-bias plots for two different viewing platforms, (a) Reader 1 and (b) Reader 2. The 1:1 line is included for reference to illustrate how the plot would look if there were complete concordance in age estimates between readers.

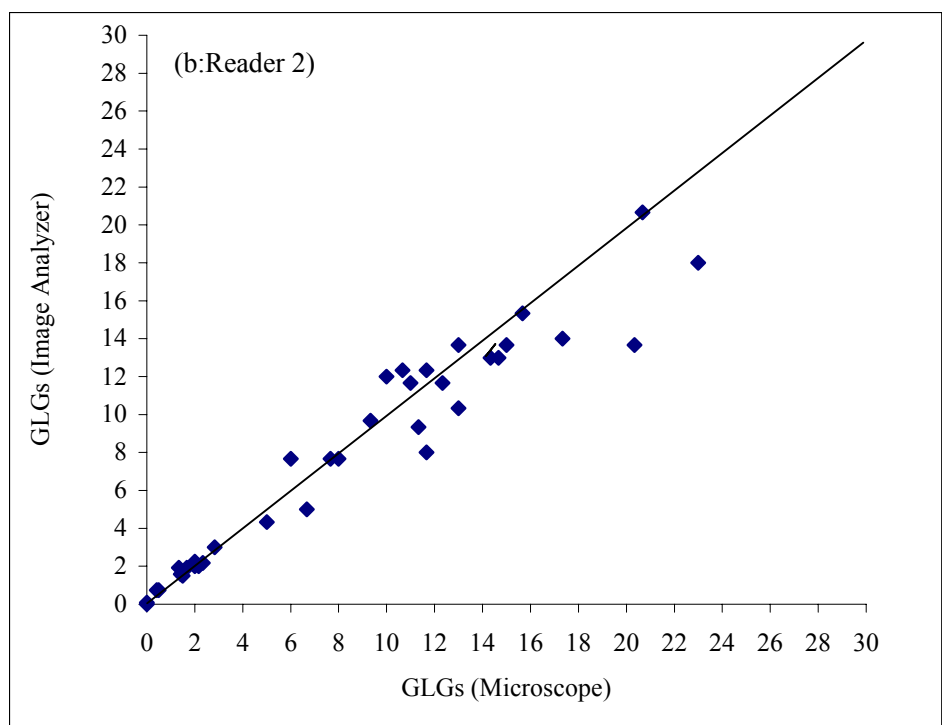
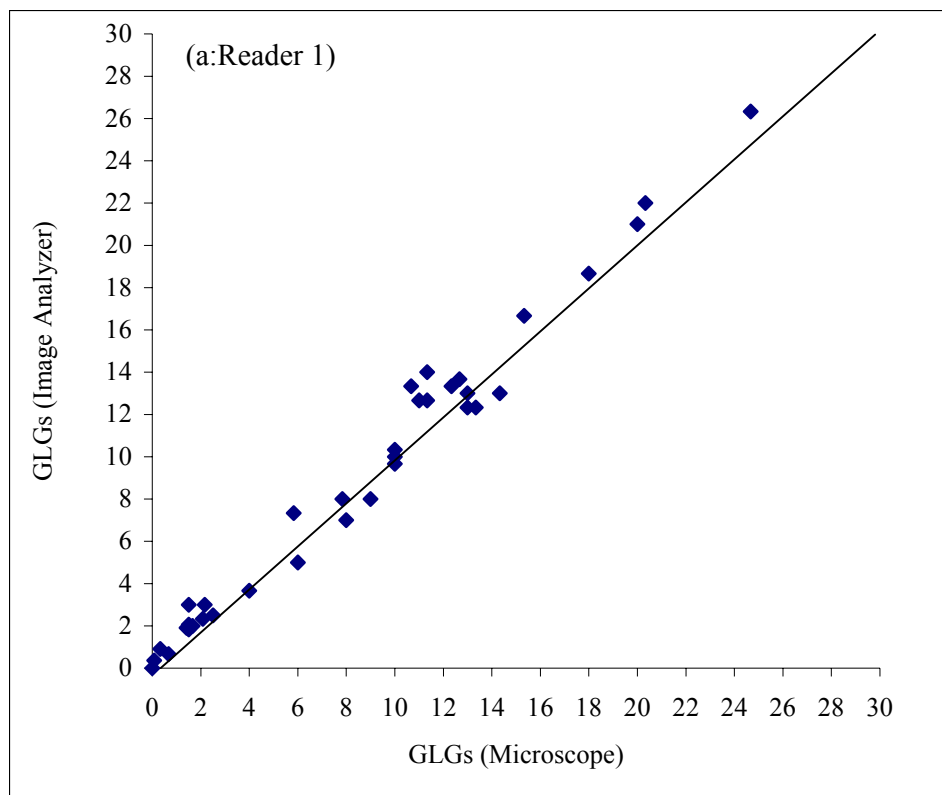


Table 7. ANOVA summary for differences in GLG counts between platforms by age class groups: 0-9 and 10+ for Reader 1 and Reader 2.

Reader 1					
Source	Sum-of-squares	df	Mean-square	F-ratio	P
Age Group	3.053	1	3.053	3.277	0.079
Error	31.670	34	0.932		
Reader 2					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Age Group	15.232	1	15.232	5.257	0.028
Error	98.516	34	2.898		

microscope (Table 8). This difference in reader behavior may stem from individual comfort level and behavior on the different viewing platforms. Reader 1 had limited aging experience on the microscope and developed the protocols for using the image analyzer, and therefore was more at ease using the computerized system. However, Reader 2 was very experienced at aging teeth on the microscope and had little experience with the computerized system and was therefore less at ease with this system. The CVs and Ds obtained on each reader's "stronger" viewing platform were similar to values reported by other odontocete aging studies (Reilly et al. 1983; Evans et al. 2002). However, CVs for ages estimated on each reader's "weaker" viewing platform were higher than published values (Table 8). Although these trends were not significant, they suggest that readers need to become experienced and comfortable using the viewing platform before readings from a new platform are used in an age-related study.

Precision in GLG counts did not change with increasing number of GLGs. While a similar observation was made during a study of sperm whales (Evans et al. 2002), my results were not expected because results of another small delphinid (*S. attenuata*) aging study found a decrease in precision with increasing GLGs (Reilly et al. 1983). Conflicting results of precision variability with age have been found in pinnipeds as well (Lawson et al. 1992; Bernt et al. 1996), suggesting that precision variability with age may vary by species (i.e., older *S. attenuata* are likely more difficult to age than sperm whales, primarily because of the size of the tooth). *D. delphis* teeth are similar in size to *S. attenuata* teeth and by analogy, aging older *D. delphis* should be comparable to *S. attenuata*.

Table 8. Calculated estimates of precision for individual readers using different viewing platforms are compared to two other odontocete age studies that estimated precision.

	Reader 1		Reader 2		Reilly et al.		Evans et al.	
	CV	D	CV	D	CV	D	CV	D
Microscope	11.70	6.75	11.53	6.66	6.90- 11.28	4.55- 6.59	10.6	4.8
Image Analyzer	9.00	5.20	14.37	8.30				

However, the similar precision across age groups found in this study implies that GLGs in older *D. delphis* teeth might be less compacted or distorted and thus have a more consistent layering pattern than other species have. The teeth used in this study may also have better defined layers due to the temperate habitat they were collected from. Variation in diet and growth, typical of seasonal habitats, may lead to more distinct layering in the teeth (Klevezal 1980).

The high CVs for the total pooled mean age estimates on both viewing platforms were similar to that reported by Reilly et al. (1983) and are likely due to reader differences in interpretation of the layering patterns of later GLGs. Future work with older known-age specimens to determine the correct interpretation of layering patterns could ameliorate large pooled mean CVs by reducing the large contribution from inter-reader differences. Unfortunately, the availability of older captive *D. delphis* teeth is low, and conducting long-term studies of wild populations are nearly impossible due to the pelagic nature of this species.

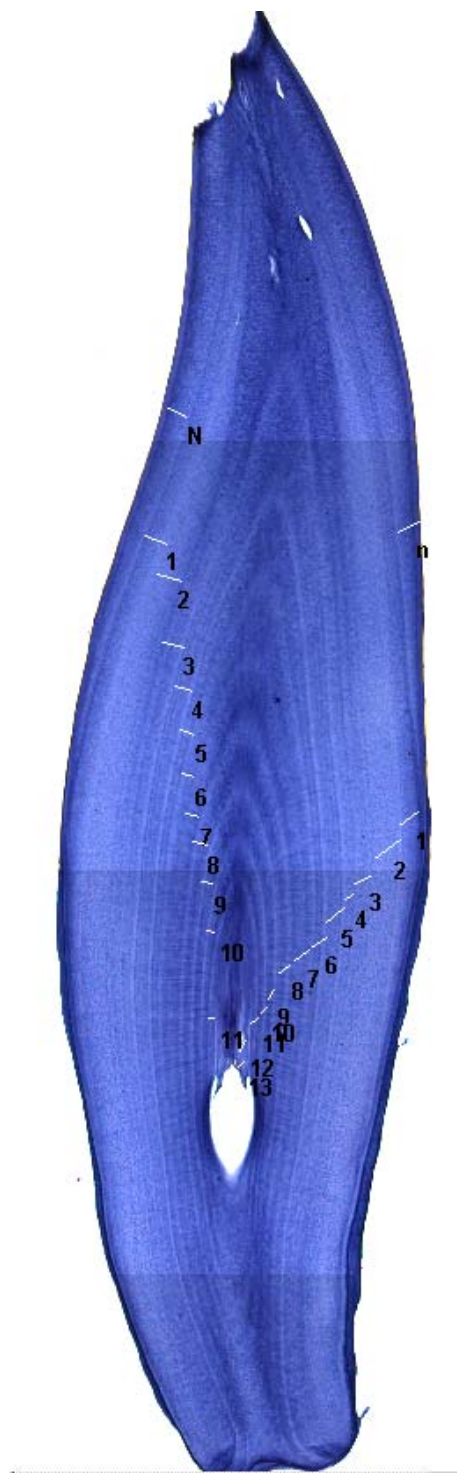
Matched paired *t*-tests and age-bias plots (Figure 4) indicated that GLG counts were more comparable between readers on the microscope than on the image analyzer. However, a slight negative bias in Reader 2 GLG counts (relative to Reader 1) for specimens between four and nine GLGs is apparent on both viewing platforms. Using image analyzer files, GLG demarcations between readers were compared on younger specimens to provide insight into potential reasons for this trend. One explanation may be that Reader 1 counted accessory lines as growth layers (thus estimating more GLGs) in the younger animals

because they are more pronounced in the characteristically wider GLGs typical of younger ages.

Tooth image files were also examined for specimens contributing to the positive age-bias of Reader 2 compared to Reader 1 (Figure 4) on both viewing platforms. A total of three teeth were responsible for the positive bias on the image analyzer. Pearling, unusual shapes, or shredded areas of the pulp cavity were present in these teeth, which may have made it more difficult for the less experienced person (Reader 1) to interpret these inner GLGs, leading to an underestimation of age (Figure 6). Four teeth in addition to those mentioned above contributed to Reader 2's positive bias of middle-aged animals on the microscope. In these teeth, it is likely that what Reader 1 considered accessory lines (and therefore did not count), Reader 2 considered GLGs. Reader 2 often used layers in the cementum to help verify GLG counts in the dentine, whereas Reader 1 did not. However, Reader 2 could not use this verification method on the image analyzer because high magnification images of cementum were not taken. This is likely why the image analyzer does not have as many specimens contributing to the positive bias in middle aged animals.

The marked negative bias of Reader 2 GLG counts of older animals on the image analyzer (Figure 4b) stems from differences in reader behavior between platforms. Age-bias plots (Figure 5) illustrate that Reader 1 had a slight positive bias for older animals on the image analyzer compared to the microscope and Reader 2 counted fewer GLGs in older animals on the image analyzer. These

Figure 6. GLG demarcations of Reader 1 (left) and Reader 2 (right) for specimen JYB0021. Note increased number of GLGs towards pulp cavity (center) by Reader 2.



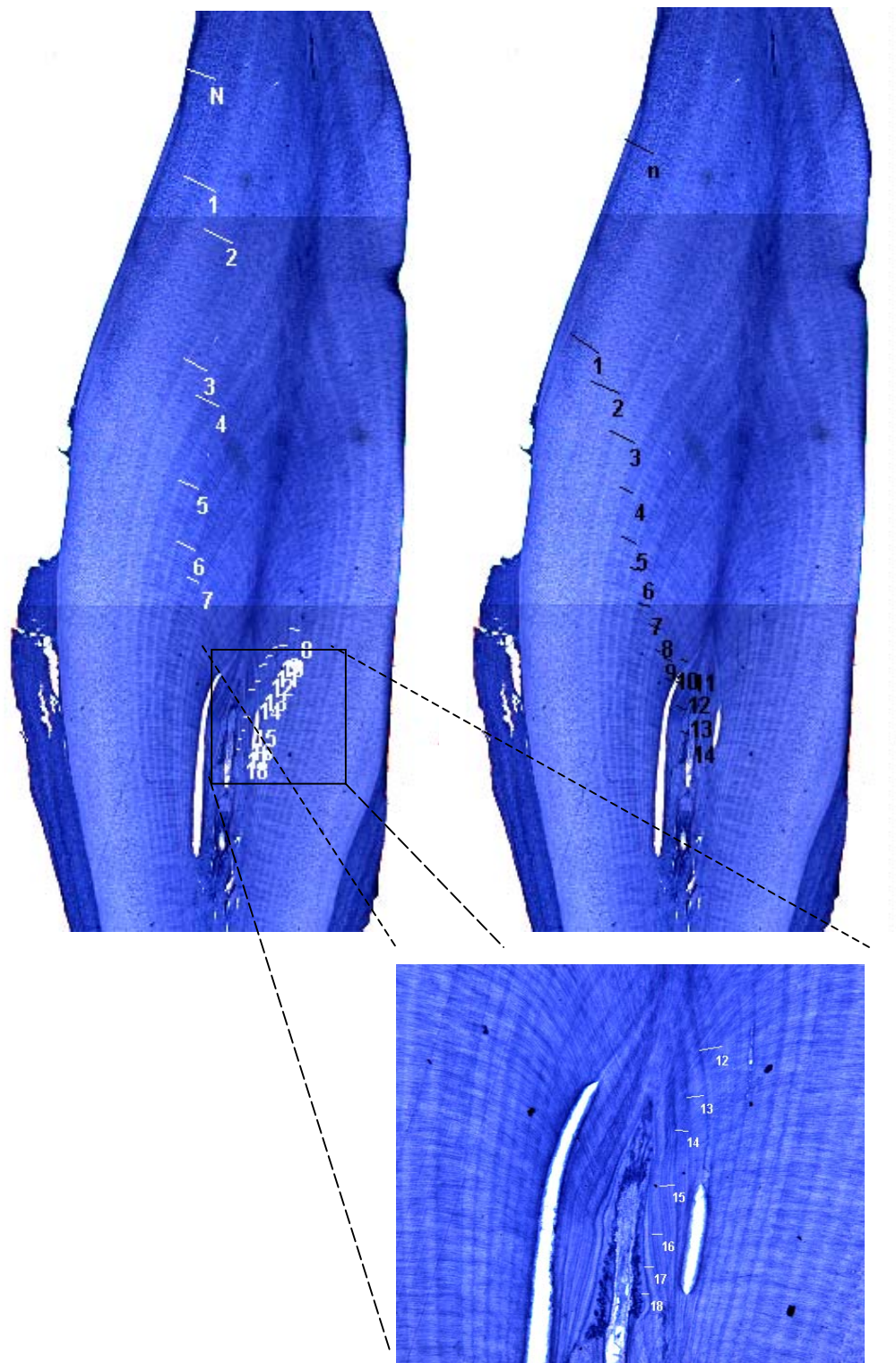
trends are likely due to Reader 2 routinely using a higher magnification on the microscope to count these inner GLGs, whereas Reader 1 rarely did this because she was less experienced tracking GLG lines when switching over to a higher objective. Interestingly, Reader 1 began routinely using a higher magnification to count inner GLGs on the image analyzer, because images on two different objectives could be viewed simultaneously, and therefore tracking GLGs between objectives was easier for this reader.

The increased use by Reader 1 and the decreased use by Reader 2 of the higher objective on the image analyzer is likely the cause for the negative bias of Reader 2 GLG estimations compared to those of Reader 1 (Figure 4b). This is supported by examination of marked GLG image analyzer files for older specimens; Reader 1 observed and marked more GLGs near the pulp cavity than Reader 2 (Figure 7), and fewer discrepancies between readers were noted in the identification of the outer GLGs. These opposing trends in age-bias on the image analyzer for the two readers (Figure 5) essentially magnify the difference in GLG counts between readers in older specimens (Figure 4b).

Potential implications of aging biases

This study showed not only that biases in aging may exist between aging platforms, but that there also several factors that may bias age estimates independent of platform. Accessory lines, tooth section condition, and GLG compaction can all influence how GLGs are interpreted. Age distributions generated from aging data could potentially be skewed depending on the degree and direction of a particular bias. A skewed age distribution could then bias estimates of age at attainment of sexual maturity as well as longevity.

Figure 7. GLG demarcations of specimen SHB003 by Reader 1 (left side with lower inset of higher magnification) and Reader 2 (right side). Note greater number of GLGs towards pulp cavity (center) for Reader 1.



Unfortunately, the degree and direction of a bias from “true” age is not often known.

Conclusions

Comparable precision to traditional light microscopy, ability to reference GLG demarcations to resolve reader differences in age, and use as a storage medium resistant to fading make digital microscope images in combination with image analysis software a promising tool for GLG estimation in small delphinid teeth. However, before this system can be used as a standard procedure for age related studies, additional analyses similar to this need to be performed after readers have gained sufficient experience with the system and a standard protocol is in place for using higher objectives and cementum layers to aid in GLG estimation of older animals. If GLG counts in the cementum are needed to verify GLG counts in the dentine, high magnification images of the cementum should be taken. If reader behavior were comparable after such protocols were implemented and experience was gained, image analysis would be the preferred method for aging delphinid teeth.

CHAPTER 4: GROWTH AND REPRODUCTION OF FEMALES

Introduction

In the ETP, research on *D. delphis* has been limited to stock structure, reproductive rates, and timing of reproduction (Henderson et al. 1980; Perryman and Lynn 1993; Dizon et al. 1994). Using data from 1973 to 1978, Henderson et al. (1980) summarized reproductive phase lengths and pregnancy rates for females of the central stock, whose boundaries differed slightly from those currently used and described in Perrin et al. (1985). Using current stock boundaries, Perryman and Lynn (1993) described patterns in timing of reproduction for all three stocks, using aerial photogrammetry.

However, the literature is incomplete and does not contain any estimates of length at birth, average age and length at attainment of sexual maturity, individual growth rates, senescence, and longevity of *D. delphis* in the ETP. The purpose of this paper is to describe the life history of females from the central stock of *D. delphis* in the ETP. In addition to presenting estimates of growth and reproductive parameters, I compare the life history parameters to those described for the species in the North Pacific (Ferrero and Walker 1994) and to other small, pelagic dolphins (*S. attenuata* and *S. longirostris*) inhabiting the ETP.

Methods

Specimen and Data Collection

Scientific observers from the NMFS and the Inter-American Tropical Tuna Commission (IATTC) collected field and biological data from dolphins

incidentally killed in the tuna purse seine fishery. Specimens were processed using the methods of Perrin et al. (1976a). Total body length of animals was measured to the nearest centimeter. Mammarys were examined for the presence of milk, reproductive tracts were collected and preserved in 10% formalin, and teeth were collected from the left lower jaw at midlength. Biological data and tissue samples were only collected from a subset of the observed kill.

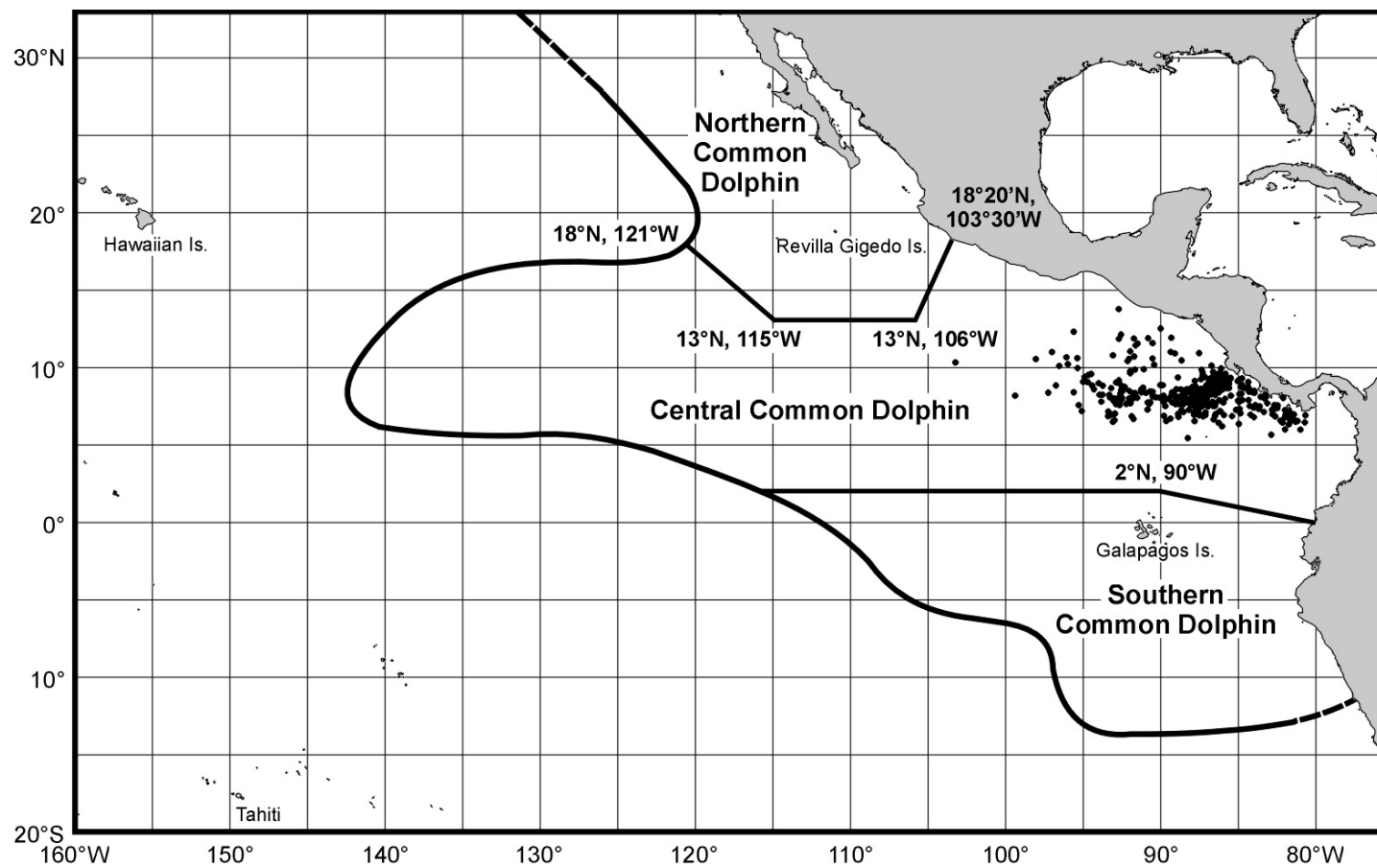
In the laboratory, ovaries were weighed and examined for the presence of *corpora lutea* and/or *corpora albicantia*. If present, these were then counted and classified as described by Akin et al. (1993). Total *corpus* count was defined as the number of *corpora albicantia* and *corpora lutea* present on both the left and right ovaries. Females were considered to be sexually mature if their total *corpus* count was greater than zero. The reproductive tract was inspected carefully for the presence of a fetus, especially if a *corpus luteum* was present. Fetuses were sexed, weighed and measured (Akin et al. 1993).

Total body length, collection date, and collection location were recorded for 1,330 female *D. delphis* collected between 1973 and 1993 (Figure 8). Age and reproductive status were determined for 506 and 880 of these specimens, respectively.

Tooth Preparation and Examination

Following the protocol of Myrick et al. (1983), teeth were decalcified, cut with a freezing microtome into 25 μm -thick longitudinal serial sections, and stained with hematoxylin. Sections were mounted on gelatin-coated slides, and cover slip margins were sealed with DPX mounting medium (Lockyer 1995).

Figure 8. Collection locations of 1330 central stock female *D. delphis* sampled.



Ages were determined by GLGs in the dentine (Myrick et al. 1983; Hohn et al. 1989) under a compound light microscope at 40x and 100x magnification. Each GLG is interpreted as representing one year of life on the basis of the calibration study by Gurevich et al. (1980).

Two readers aged each tooth three times, with at least a week between readings. GLG counts were made without reference to specimen information, such as total body length, reproductive status, or previous GLG counts. The mean GLG count of both readers' three readings is referred to as the total pooled mean age estimate, whereas the mean for an individual reader is referred to simply as mean age estimate. Pooled mean age estimates were used in all analyses of reproduction and individual growth data. Coefficient of variation ($CV = \frac{SD}{\bar{X}} \times 100$) was used to measure the precision of age estimates (Chang 1982).

Stable Age Distribution

A predicted stable age distribution was generated using the proportion of animals expected in each age class based on a leslie matrix model using spinner dolphin age-specific survival rates (Chivers 2002b).

Length and Age Parameter Estimation

Three methods were used for estimating length at birth and age and length at attainment of sexual maturity: (a) the sum-of-fraction-immature method (Hohn 1989), (b) the DeMaster (1978) method, and (c) logistic regression. These methods were used as a means to compare parameters to other studies and to determine the best estimator for this study.

Sum-of-fraction immature method

The sum-of-fraction immature (SOFI) method estimates the average age at attainment of sexual maturity (ASM) as

$$ASM = j + \sum_{i=j}^k p_i x_i, \quad (1)$$

where j is the age of the youngest mature animal, k is the age of the oldest immature animal, p_i is the proportion of immature animals in age class i , and x_i is the number of age classes combined in age class i . Variance was estimated as

$$\text{var (ASM)} = \sum_{i=j}^k \frac{p_i(1-p_i)x_i}{n_i - 1}, \quad (2)$$

where n_i is the sample size for age class i .

To estimate average length at attainment of sexual maturity (LSM), the SOFI method was modified to use constant length intervals (5 cm) instead of ages so that

$$LSM = j + \sum_{i=i_{\min}}^{i_{\max}} p_i x_i, \quad (3)$$

where j is the lower limit of the length class with the smallest mature animal, i_{\min} is the length class with the shortest mature animal, i_{\max} is the length class with the longest immature animal, p_i is the proportion of immature animals in length class i , and x_i is the number of age classes combined in age class i . Variance was estimated as

$$\text{var (LSM)} = \sum_{i=i_{\min}}^{i_{\max}} \frac{p_i(1-p_i)x_i}{n_i - 1}, \quad (4)$$

where n_i is the total number of animals in the i th length class.

The SOFI method was modified similarly to estimate average length at birth where j is the lower limit of the length class with the smallest calf, i_{min} is the length class with the smallest calf, i_{max} is the length class with the longest fetus, p_i is the proportion of fetuses in length class i , x_i is the interval width of length class i , and n_i is the total number of animals in the i th length class.

Demaster Method

Using the DeMaster method (1978), ASM was calculated as

$$ASM = \sum_{i=j}^k i(p_{mi} - p_{mi-1}), \quad (5)$$

where j is the age of the youngest mature animal, k is the age of the oldest immature animal, p_{mi} is the proportion of mature animals aged i . The variance was estimated as

$$\text{var}(ASM) = \sum_{i=j}^k \frac{p_{mi}(1 - p_{mi})}{n_i - 1}, \quad (6)$$

where n_i is the total number of animals aged i .

The DeMaster method was modified to use lengths grouped into 5-cm intervals instead of ages so that

$$LSM = \sum_{i=j}^k l_i(p_{mi} - p_{mi-1}), \quad (7)$$

where j is the length class with the smallest mature animal, k is the length class with the largest immature animal, l_i is the lower limit of the i th length class, and p_{mi} is the proportion of mature animals in the i th length class. The variance equation was modified to account for constant interval width (Ferrero and Walker 1993; Ferrero and Walker 1994) and was computed as

$$\text{var (LSM)} = w^2 \sum_{i=j}^k \frac{p_{mi}(1-p_{mi})}{n_i - 1} \quad (8)$$

where w is the constant interval width and n_i is the number of animals in the i th length class.

Since negative values of p_{mi} were present in the length and age datasets, new predicted proportions were calculated from a nonlinear curve fitted to a plot of proportion mature versus age and length (Laws et al. 1975) and entered into the models.

Logistic Regression

Logistic regression analysis, based on maximum likelihood, was used to estimate ASM and LSM by determining the length and age at which 50% of a combined sample of immature and mature animals was predicted to be mature. Similarly, logistic regression was used to determine estimated length at birth (ELB) by determining the length at which 50% of a combined sample of fetuses and post-natal specimens was predicted to be born. To increase sample size, both males and females were used to estimate length at birth. Confidence intervals were constructed based on 1,000 bootstrap replicates conducted by sampling the data with replacement.

To determine whether the calculated mean length at birth is significantly biased by undocumented calf mortality (i.e., missing calves in the data set; Archer et al. 2001), an alternative estimate of length at birth was calculated (using the logistic regression method) based on a hypothetical data set and then compared to the original estimate. The hypothetical data set added 15% more (+8) calves,

which is the upper range of undocumented mortality estimated by Archer et al.(2001), to the smallest indeterminate length class (75 cm).

To test the null hypothesis that the original ELB and the hypothetical ELB were the same, the data sets were permuted, and a P-value calculated for the comparison. The permuted data sets were created by pooling the original and hypothetical data sets, then creating 1000 new data sets of two groups (with original n) through random sampling of the pooled group. The P-value is the proportion of the runs that the difference in ELB between the permuted data sets was greater than or equal to the observed difference between the original and hypothetical data set.

Comparison of methods

For this study, the preferred method for calculating ASM, LSM and ELB is the logistic regression followed by the SOFI method. The DeMaster method was least favorable because of the need to calculate new predicted proportions that the variance calculation does not take into account. The advantage of the SOFI and logistic methods was that they could be used with the original raw data set. However, the binning required for the SOFI method likely results in a loss of resolution, and the associated variance appears to be underestimated. The ability to input raw data and to capture the variance of the fit with bootstrap replicate sampling makes the logistic regression method preferable and it is thus used in all parameter comparisons in this study.

Age at conception and first birth

Age at conception was calculated by subtracting the age of the fetus (estimated from fetal length; see Table 9) from the age of the female on the day of

Table 9. Age of conception was calculated for pregnant females with one *corpus luteum* and no *corpora albicantia*. Fetus age was based on fetal growth model developed by S. Chivers.

SPECIMEN	Age on day of collection (years)	Age of conception (mother's age - fetus age) (years)	Fetus Length (cm)	Fetus Age (days)	Fetus Age (years)
JEJ0021	9.2	9.2	0.1	2	0.006
TBS0216	10.8	10.8	0.5	5	0.014
MAK0241	9.2	9.0	16	79	0.216
PLR0022	8.0	7.8	16.3	80	0.219
JHT0074	9.5	9.2	19.5	92	0.252
RWC0469	6.8	6.3	49	202	0.553
REB0033	10.8	10.0	78	317	0.869
RJO0384	8.3	7.5	78.2	318	0.871
WCF0105	14.0	13.1	80	325	0.890
WCF0098	9.8	8.9	85	344	0.943

collection. This calculation was based on pregnant females with one *corpus luteum* and no *corpora albicantia* and excluded one 16-year-old, considered to be an outlier in the data set. Mean age at first birth was estimated using only the lactating females with one *corpus*.

Gestation

Gestation was estimated using Perrin et al.'s (1977) regression equation,

$$\text{Log } (y) = 0.1659 + 0.4856 \text{ Log } (x), \quad (9)$$

where y is the length of gestation and x is the length at birth. This equation is based on the positive correlation between length at birth and gestation of four closely related delphinids.

Growth

Using the Laird-Gompertz formula (Laird 1969), a two-phase growth model (Perrin et al. 1976a; Perrin et al. 1977) was used to simultaneously fit separate equations to female age at length data, using an iterative least-squares method. The Laird-Gompertz model is

$$L(t) = L_o * e^{(a(1-e^{(-\alpha t)}))} \quad (10)$$

where $L(t)$ is length at time t , L_o is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth. The first model was anchored at the ELB. The intersection point of the two models was estimated as the age at which the total sum of squares for the fit of both models was smallest.

Seasonality

Birth dates for animals estimated to be less than one year old (i.e., total length ≤ 134 cm) were back-calculated using,

$$d_b = d_c - 30 \frac{l_c - l_b}{r} \quad (11)$$

where d_b is the day of the year of the birth date, d_c is the day of the year of collection, l_c is the length at collection, l_b is length at birth, and r is growth rate in centimeters per month. The ELB derived from the logistic method was rounded down and used as an estimate of l_b . The growth rate of 4.1 cm/month obtained from the previously described growth model was used as the estimate for r .

Reproductive Phases and Calving Interval

The proportion of pregnant, lactating, and resting (those neither pregnant or lactating) females (Table 10) was used in combination with the gestation period to determine estimates of the calving interval (Perrin et al. 1976a). The summation method (gestation + lactation + resting phases) and the reciprocal of the APR were used to calculate two estimates of calving interval (Perrin et al. 1976a). Both of these methods are based on the likely invalid assumption of no fetal mortality (Perrin et al. 2003). The equations for estimating time spent lactating and resting, and APR are:

$$\text{Lactation} = \frac{L}{P} \times G \quad (12)$$

$$\text{Resting} = \frac{R}{P} \times G \quad (13)$$

$$\text{APR} = \frac{P}{G} \quad (14)$$

where, L is the proportion of sexually mature females lactating (including those simultaneously pregnant), P is the proportion of sexually mature females pregnant

Table 10. Reproductive condition of 440 sexually mature female *D. delphis* collected between 1973 and 1993.

Condition	Number	Percent
Pregnant only (P)	119	27.1
Lactating only (L)	199	45.2
Pregnant & Lactating (PL)	73	16.5
Resting	49	11.1
Total sexually mature females	440	

(including those simultaneously lactating), G is the length of gestation in years, and R is the proportion of sexually mature females neither pregnant nor lactating.

Results

The Sample

To assess potential subsampling biases of the aged and reproductive samples, the length frequency distributions of these subsamples were compared to that of the total sample. The median length value of these subsamples (191 cm and 189 cm) were within the median 95% confidence interval (143 - 202.5 cm) of a bootstrap replicate sample of 1000 (based on the total sample), indicating that these were random subsamples of the entire sample. Lengths and ages of female *D. delphis* ranged from 84 to 213 cm (Figure 9) and 0 to 25 years (Figure 10), respectively. The age distribution is bimodal (Figure 10), with peaks in the age classes of juveniles (i.e., three and four year olds) and sexually mature adults (i.e., 11 to 13 year olds). This is quite different from what is expected under a stable age distribution (Figure 10). For delphinids, the greatest frequency of animals is expected to be neonates, followed by yearlings, juveniles, and adults (Figure 10).

Aging

The calculated CVs for Reader 1, Reader 2, and the pooled mean age estimate were 17.3%, 14.0%, and 21.0%, respectively. A Spearman rank correlation test for each reader indicates that there is no relationship between CV and mean age estimate (Reader 1, $P = 0.610$; Reader 2, $P = 0.658$). Between readers, 58 % of readings agreed to within one year and 76% agreed to within two years. Mean age estimates were not significantly different between readers

Figure 9. Total body length frequency distribution of central female *D. delphis* sampled ($n = 1330$). The x-axis labels represent the upper bound of the length interval.

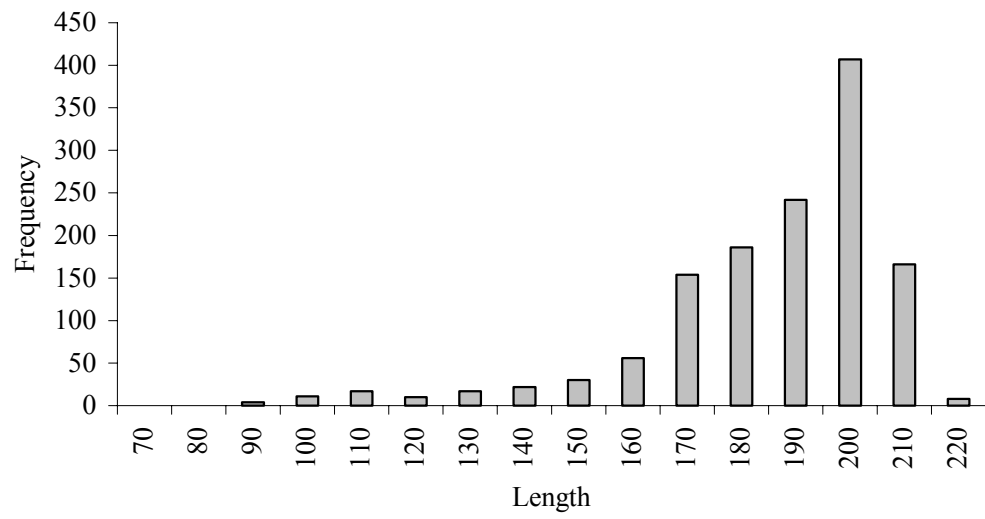
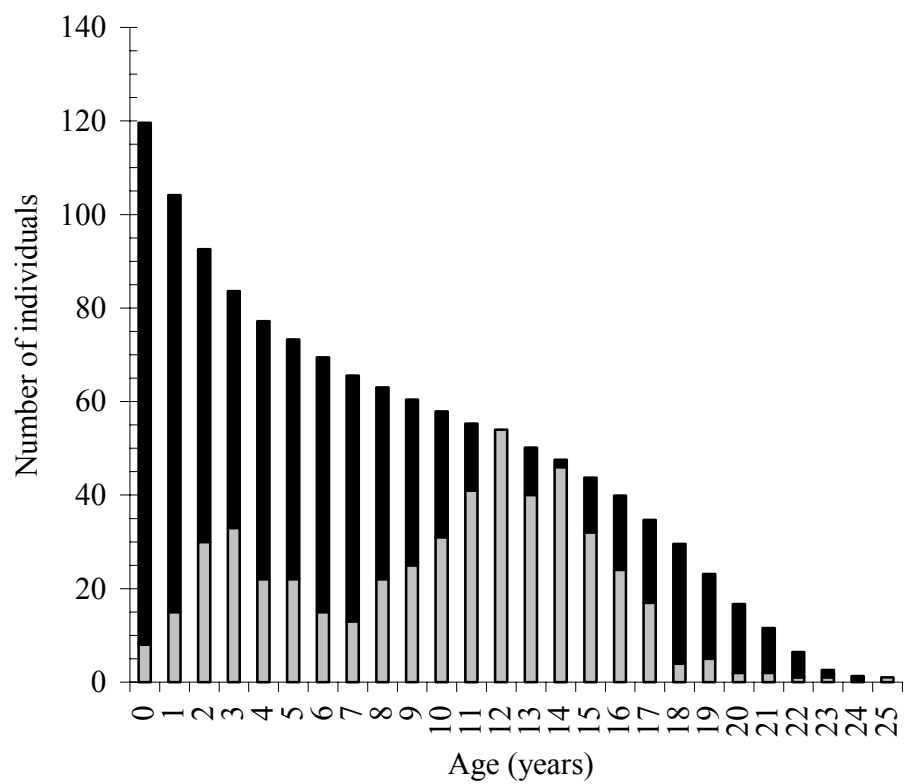


Figure 10. Age frequency distribution of sampled central female *D. delphis* (gray bars only; n = 506) and predicted stable age distribution (gray + black bars) typical for small delphinids.



(Wilcoxin Signed-Rank Test: $z = 0.627$, $P = 0.531$). However, a plot of age differences between readers illustrates that compared to Reader 1, Reader 2 tended to estimate higher for younger animals and lower for older animals (Figure 11).

Length at Birth

The smallest calf was 75 cm long and the largest fetus was 88 cm. The mean length of the 19 fetuses and 9 calves within that length range (Figure 12) is 82.7 cm ($n = 28$; 17 male, 11 female, $SE = 0.732$).

Using logistic regression (Figure 13) and a modified SOFI method based on 5-cm groupings, ELBs are 85.2 cm (95% CI, 82.9-87.1) and 85.5 cm ($SE = 0.092$), respectively. All female postnatal specimens, male postnatal specimens ≤ 98 cm, and fetuses (regardless of gender) with an associated total body length were used in the logistic regression analysis.

Gestation

Using the ELB of 85.2 cm, gestation was estimated to be 11.3 months. This estimate could not be compared to the method of Hugget and Widdas (1951) because the available data violated the assumption that reproduction is seasonal. The linear phase of fetal growth required for this method could not be estimated using this data set, because fetuses of all lengths and therefore ages were present throughout the year (Figure 14).

Postnatal Growth

Growth was rapid through age 2 with predicted lengths of one- and two-year olds of 133.9 cm and 159.3 cm, respectively (Figure 15). After age two,

Figure 11. Differences in mean age estimates (years) between readers across ages. Compared to Reader 1, a positive bias in younger animals and a negative bias in older animals are present for Reader 2.

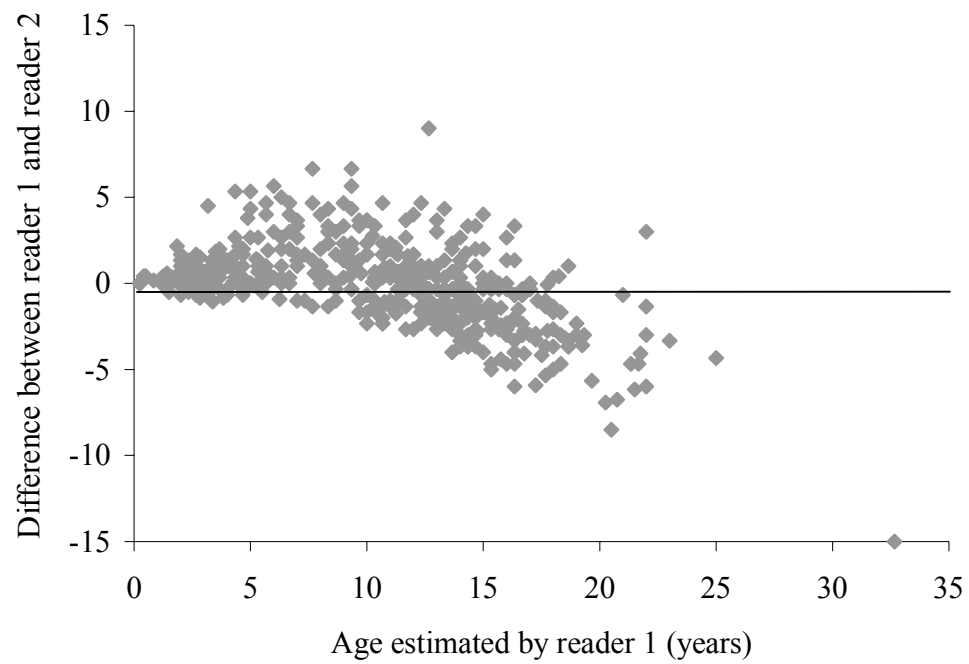


Figure 12. Length frequency distribution for 19 fetuses and 9 calves (males and females) of central *D. delphis* within the overlapping length range of smallest calf and largest fetus.

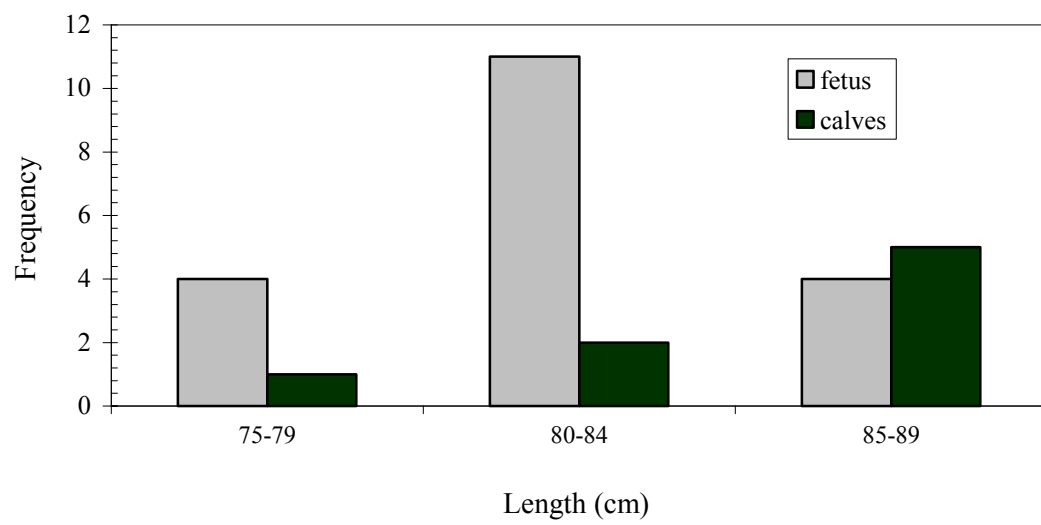


Figure 13. A logistic curve fitted to length and postnatal status. The length at which 50% of specimens are predicted to be calves equals 85.2 cm (95% CI, 82.9 - 87.1 cm), the estimated length at birth. The circles represent individual samples. Range of x-axis limited for presentation.

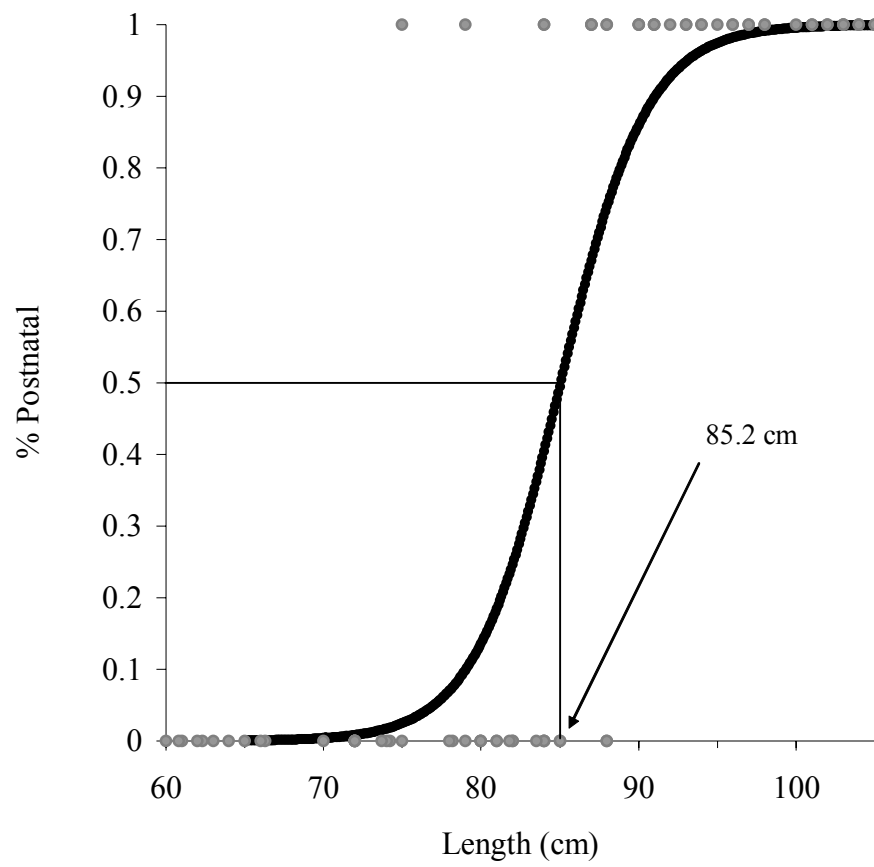


Figure 14. Scatterplot of fetal lengths and day of collection.

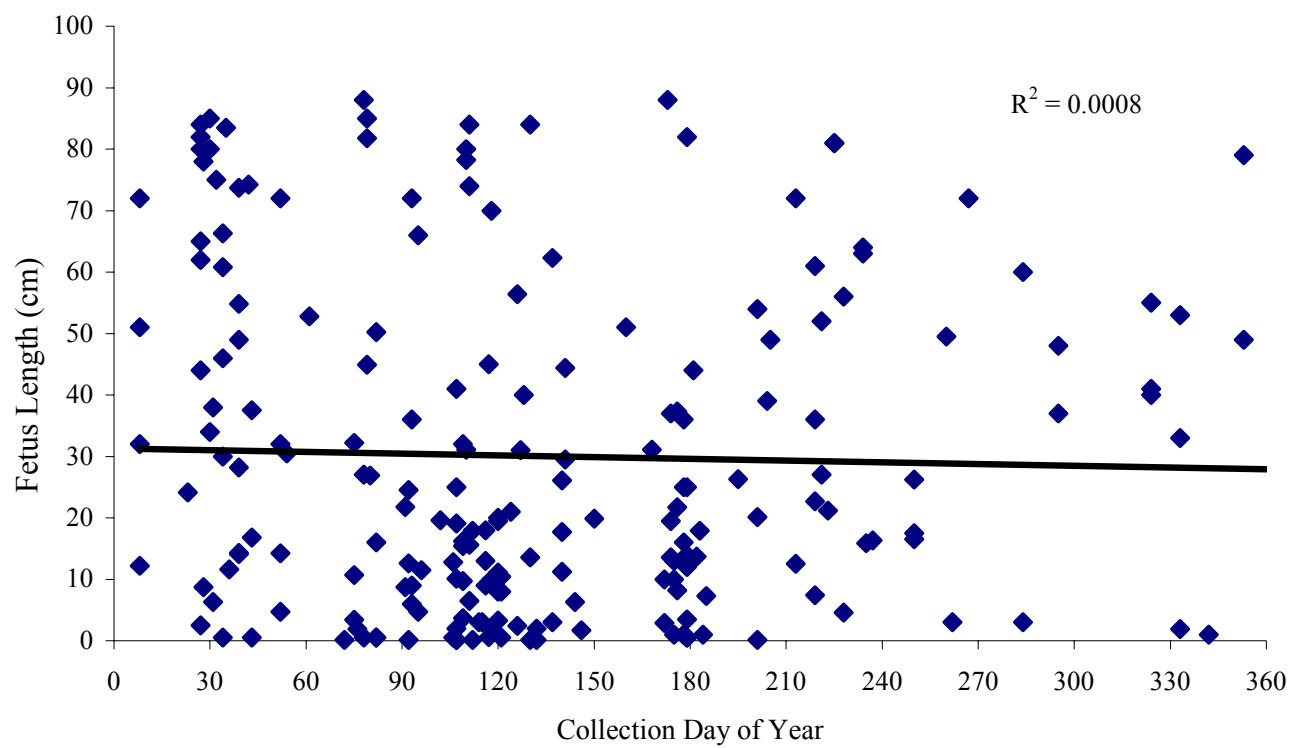
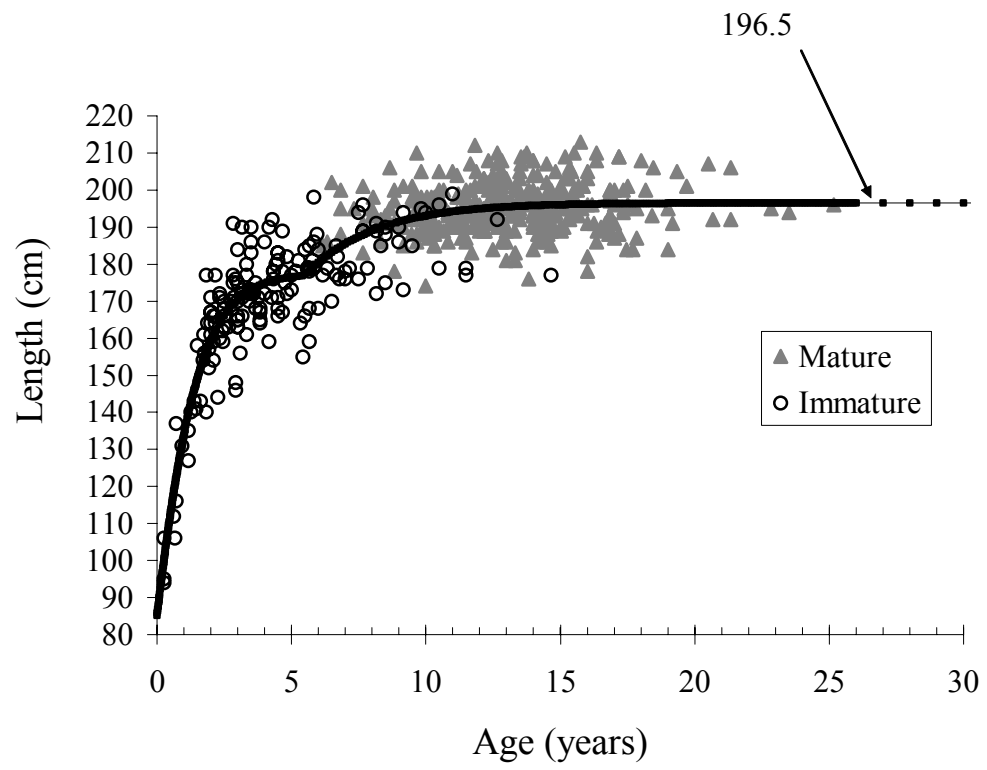


Figure 15. Two-phase Laird-Gompertz growth model fit to female *D. delphis* age at length data. The predicted asymptotic length from the model was 196.5 cm.



growth slowed until 5.48 years, where growth rate increased again. Growth subsequently slowed again until it reached an asymptote of 196.5 cm.

Sexual Maturation

The youngest sexually mature female was 5 years old and the oldest sexually immature female was 14 years old (Figure 16a). The average ASM was estimated to be 8.0 years (SE = 0.013) using the SOFI Method, 8.1 years (95% CI, 7.7 - 8.5) using the Logistic Method (Figure 17), and 8.0 years (SE = 0.013), using the DeMaster (1978) method. The mean age of first conception was estimated to be 8.7 years (n = 10, SE = 0.601). On average, females gave birth for the first time at 10 years of age (n = 10, SE = 0.791).

Length and Sexual Maturation

Sexually mature females ranged in length from 172 to 213 cm (Figure 16b) and averaged 195.2 cm in length (n = 461, SE = 0.317). The largest sexually immature female was 205 cm long (Figure 16b). Using the modified SOFI method, modified DeMaster, and logistic methods (Figure 18), length at sexual maturity was estimated to be 186.4 cm (SE = 0.008), 184.4 cm (SE = 0.018), and 185.9 cm (95% CI, 185.0-186.7), respectively.

Ovulation

Total *corpus* counts in sexually mature females ranged from 1 to 30. A regression of mean number of *corpus* scars on age class shows a significant increase in *corpus* scars with age ($P < 0.001$) (Figure 19). To fit this regression, *corpus* counts for the youngest and oldest ages were combined so that sample sizes were greater than five for the 5 and 20 year age classes. Among mature

Figure 16. Scatterplot of total *corpora* count of central female *D. delphis* as a function of (a) age ($n = 506$) and (b) length ($n = 880$).

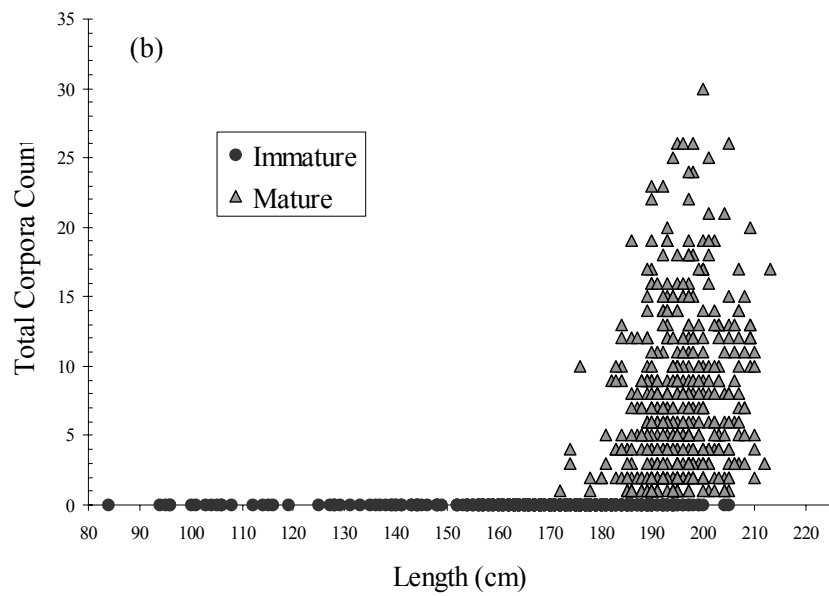
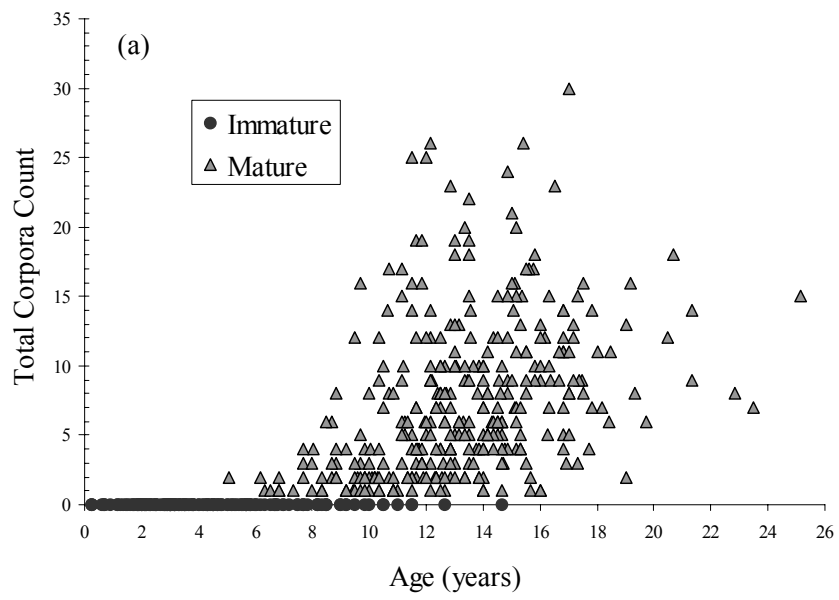


Figure 17. A logistic curve fitted to age and maturity status. The length at which 50% of specimens are predicted to be mature equals 8.1 years (95% CI, 7.6 - 8.5 years), the estimated ASM. The circles represent individual samples.

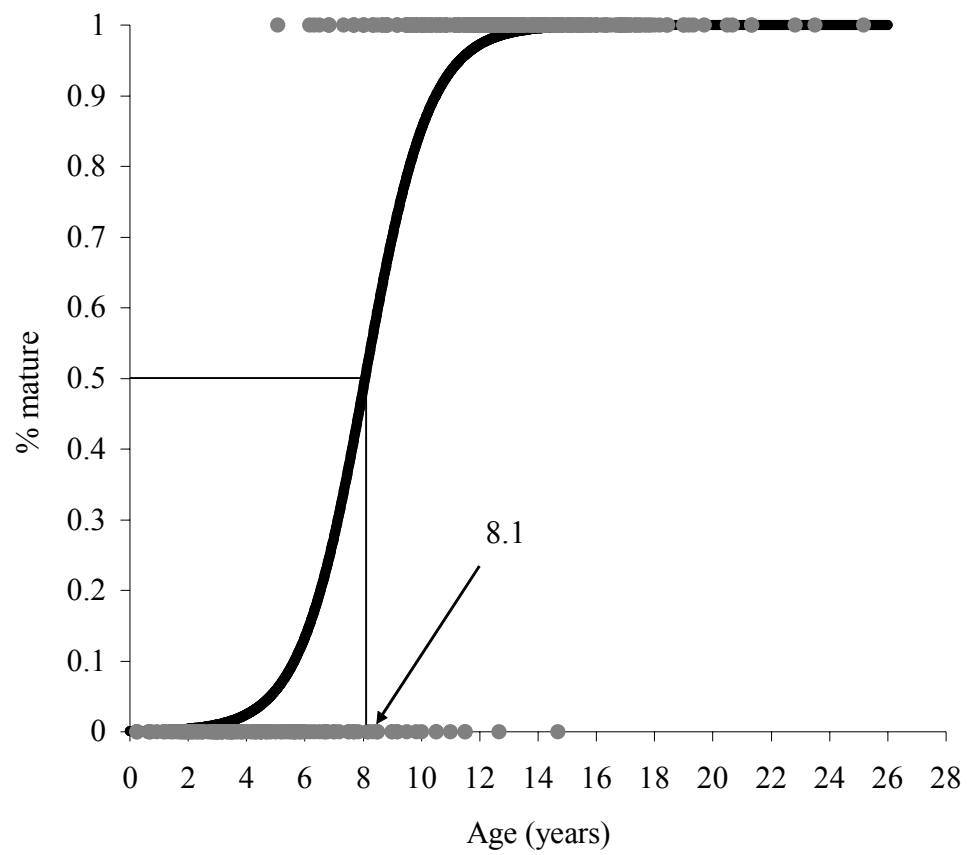


Figure 18. A logistic curve fitted to length and maturity status. The length at which 50% of specimens are predicted to be mature equals 185.9 cm (95% CI, 184.9 - 186.8 cm), the estimated LSM. The circles represent individual samples.

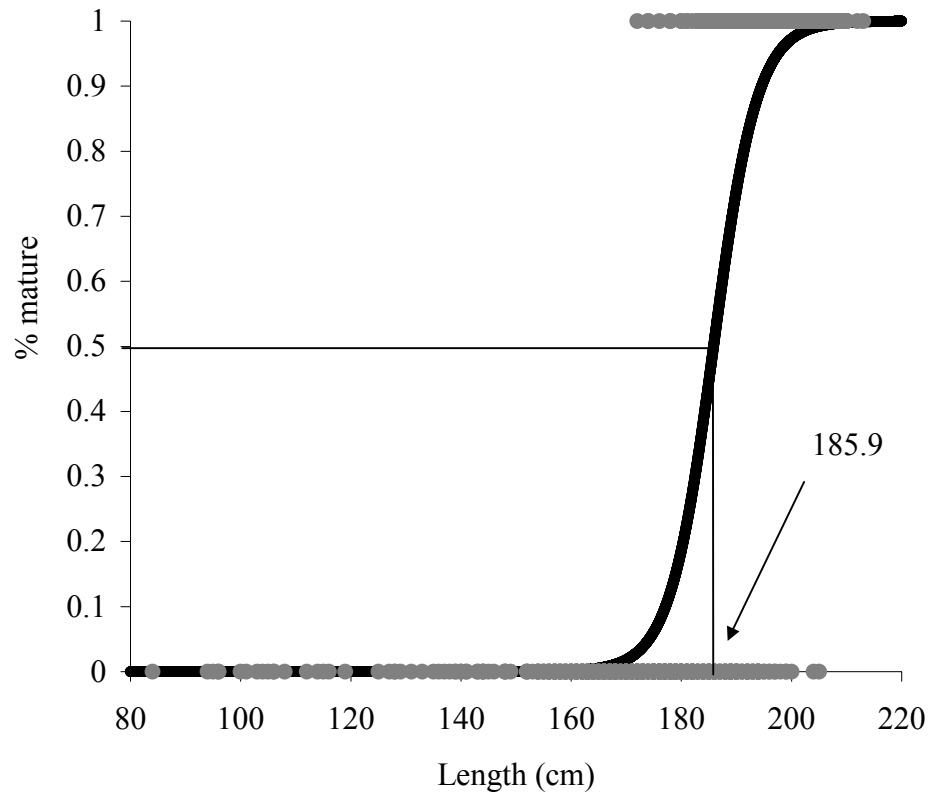
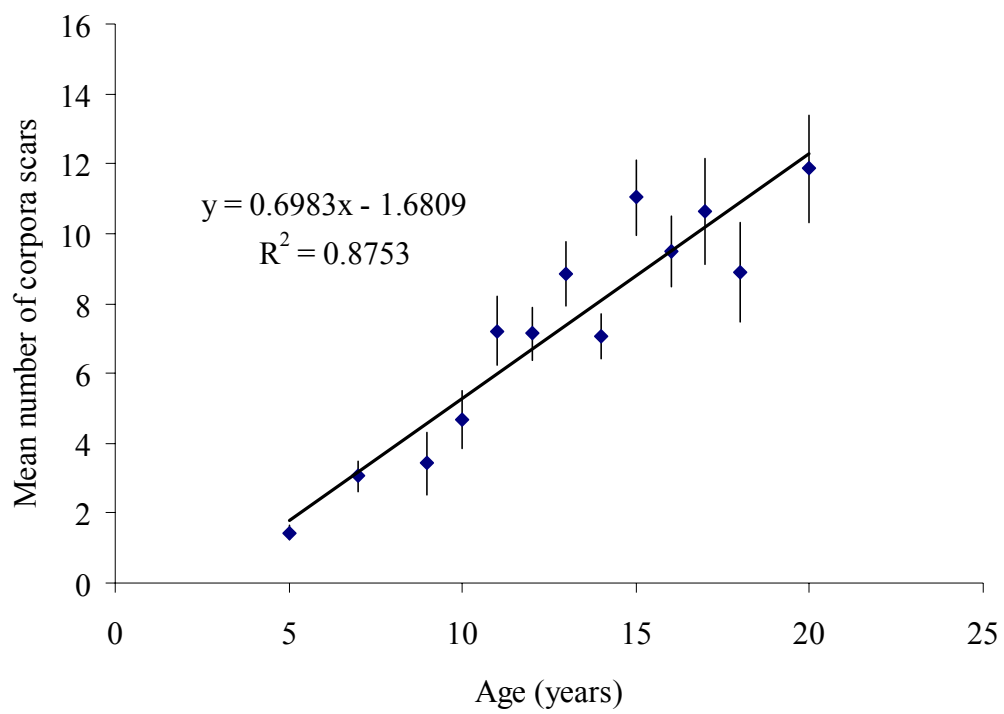


Figure 19. Mean number of *corpora* scars increases with age in central *D. delphis* ($P < 0.001$). Points represent means for one-year age classes. Vertical bars represent standard errors of the mean count for each age class.



females, the mean number of *corpus* scars was greater in the left ovary than in the right ovary (Wilcoxin Rank Sum Test: $z = -22.464$, $P = 0.0000$). In fact, at least 90% of the first three ovulations occur in the left ovary. A gradual shift to using both ovaries occurs with increasing *corpora*. After 15 *corpora* have accumulated this shift becomes more pronounced (Table 11).

Seasonality

No clear peaks in birth dates were indicated in the resulting distribution of back-calculated birth dates (Figure 20). The Kuiper's test demonstrates that birth dates were not significantly different ($K = 1.0$, $P > 0.10$) from a uniform distribution (Figure 20), indicating no seasonality in female reproduction.

Reproductive Phases and Calving Interval

The summation of the gestation (11.3 months), lactation (16.1 months), and resting (2.9 months) phases estimated a calving interval of 30.3 months, or 2.5 years. The second estimate of 25.9 months, or 2.15 years was derived from the reciprocal of the APR ($1/0.466$). This estimate of the calving interval is likely lower than that calculated from the sum of reproductive phases, because it includes 26.8 % of lactating females that are simultaneously pregnant, whereas the other calving interval estimate is the sum of the observed reproductive phases of females whose reproductive phases do not overlap. Additionally, the data set shows that pregnancy and lactation rates change with age. That is, pregnancy rate decreases with increasing age as lactation rates increase (Figure 21).

Table 11. Location of *corpora* (*corpora lutea* and *corpora albicantia*) in the ovaries of 460 central *D. delphis*.

		Location of corpora		
Corpora (no.)	Sample size (no.)	Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	38	92.1	7.9	0.0
2	58	94.8	1.7	3.4
3	36	91.7	0.0	8.3
4	42	88.1	4.8	7.1
5	33	87.9	0.0	12.1
6	30	93.3	0.0	6.7
7	28	92.9	3.6	3.6
8	27	85.2	0.0	14.8
9	28	71.4	7.1	21.4
10	23	65.2	0.0	34.8
11	12	58.3	0.0	41.7
12	20	70.0	0.0	30.0
13	14	64.3	0.0	35.7
14	12	66.7	0.0	33.3
15	12	58.3	0.0	41.7
16-17	16	37.5	0.0	62.5
18-19	14	7.1	7.1	85.7
20-30	17	11.8	0.0	88.2

Figure 20. Distribution of cumulative back-projected birth-dates. The observed cumulative distribution is not significantly different from an expected uniform cumulative distribution ($P > 0.10$), indicating no seasonality in female reproduction. Bars indicate frequency of back-calculated birth-dates of female ($n = 66$) and male ($n = 68$) *D. delphis* ≤ 134 cm.

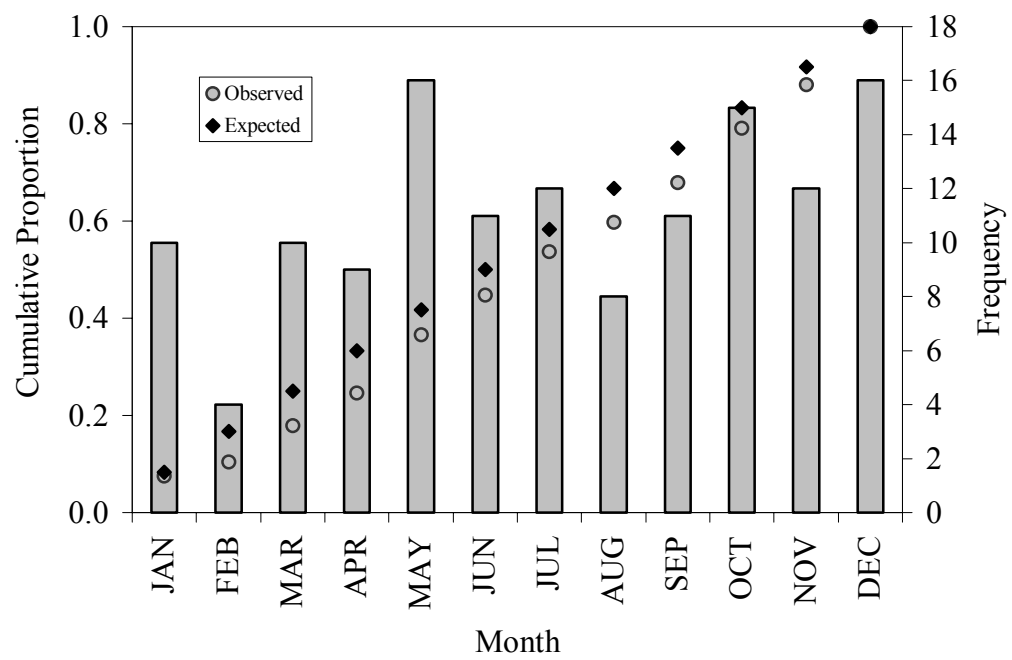
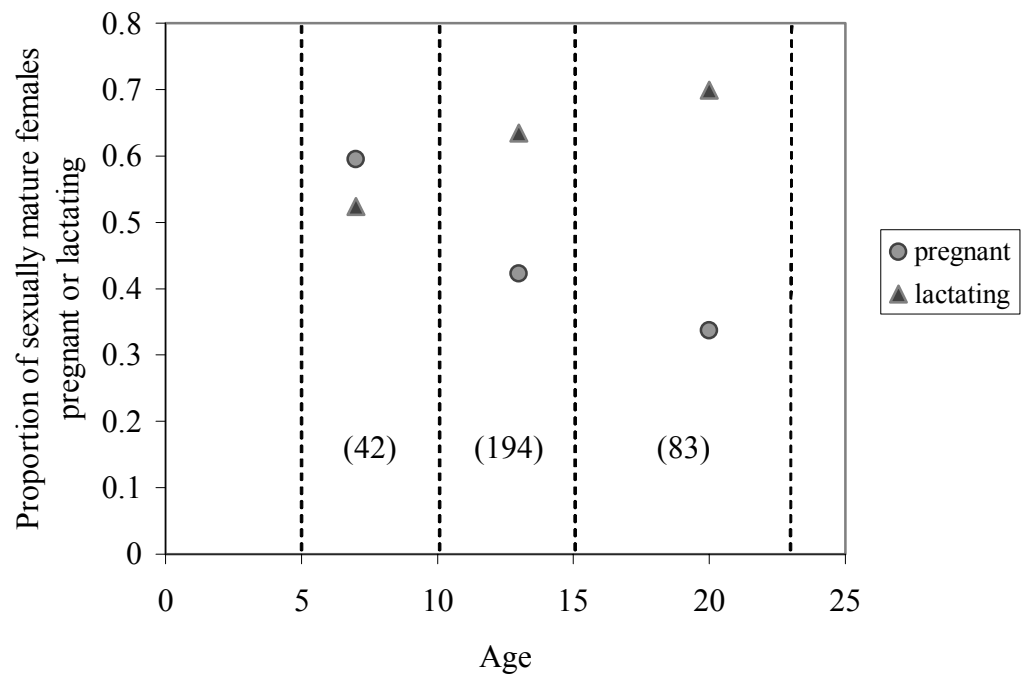


Figure 21. Plot of proportion of females pregnant and proportion lactating on age.

The proportion of pregnant females decreases with age, along with a concomitant increase of proportion lactating. Dashed lines represent how data were binned to calculate proportions, with samples sizes in parentheses.



Post-Reproductive Females

Following the criteria of Perrin et al. (1977), 440 sexually mature females were examined for evidence of senescence. The five criteria indicative of senescence are: (1) neither pregnant or lactating, (2) ≥ 10 corpora, (3) ovaries weigh < 3.5 g, (4) no developing follicles, (5) no Type 1 or 2 corpora albicantia. None of the 440 animals showed clear evidence of being post-reproductive since none met all five criteria. Ten specimens met at least three of the five criteria, and two specimens met four (Table 12).

Discussion

The age distribution of the sample is markedly different from that of female *S. l. orientalis* (Chivers 2002b) and more similar to that of female *S. attenuata* (Barlow and Hohn 1984) that inhabit the same area and are impacted by the same fishery. Both calves and juveniles are underrepresented in the age distributions of *D. delphis* (Figure 10) and *S. attenuata* (Barlow and Hohn 1984) when compared to an expected stable age distribution. Several alternative explanations for the age distribution in *S. attenuata* were outlined by Barlow and Hohn (1984), which include (a) school segregation, (b) a variable rate of tooth deposition, and (c) non-stable age distribution reflecting large perturbation in the population.

If schools are segregated by age or reproductive class, juvenile animals may inhabit different areas, or they may not join herds that associate with tuna that are targeted by the purse-seine fishery. Kleinenberg (1956) and Tomlin (1957) documented herd segregation of *D. delphis* in the Black Sea, where

Table 12. *D. delphis* specimens that possess at least three of five criteria elements indicative of senescence.

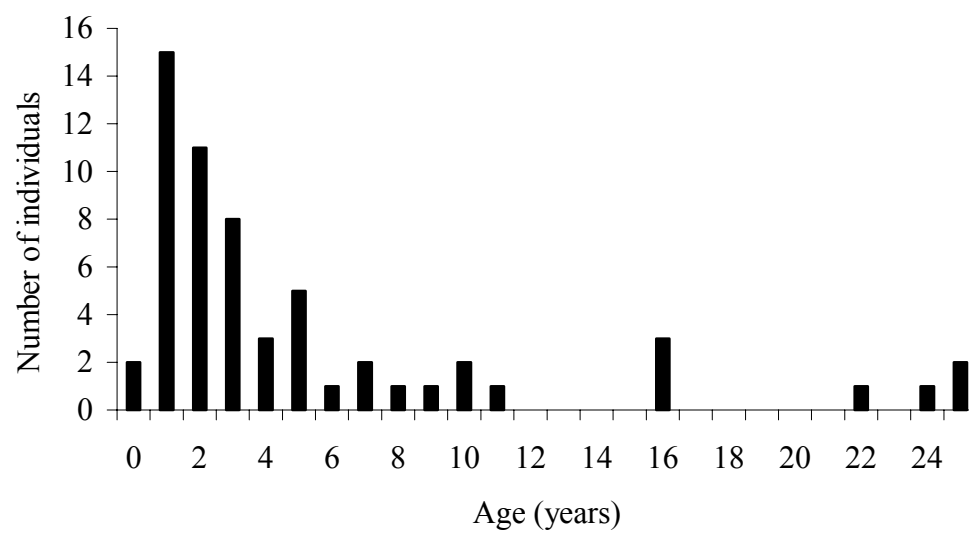
Specimen No.	Total <i>Corpora</i>	Resting	Ovaries<3.5 g	No developing follicles	No type 1 or 2 <i>corpora</i>
DAM0039	26	X	X	X	
MAJ0014	25	X	X	X	
WOK0056	13	X	X		
JJN0063	19	X	X		
REL0160	19	X		X	
JEJ0103	16	X			X
RDP0120	11	X	X		
AGA0012	26	X		X	
DJG0094	12	X			X
NWV0132	10	X	X		

females predominantly occur offshore during periods of calving and early lactation. Population segregation has been suggested for the North Pacific population of *D. delphis* (Ferrero and Walker 1994) to explain the paucity of pregnant females and neonates in their sample collected from a high-seas driftnet fishery.

Variable tooth rate deposition could lead to misinterpretations of growth layers leading to inaccurate estimates of ages. Since the age distribution of *D. delphis* in the N. Pacific (Figure 22) is quite different from that found in the ETP (Figure 10), variable tooth rate deposition for this species seems a less likely hypothesis and may reflect inherent sampling biases of the two fisheries. However, it is conceivable that tooth rate deposition could vary within a species in response to habitat or prey differences and therefore could still be a possible explanation. Exploring this explanation further is complicated because there are likely other biases or inaccuracies in reading GLGs in the teeth.

Incidental mortality in the purse-seine fishery certainly has served as a large perturbation in the population with central *D. delphis* mortality peaking at 21,299 in 1973 during the years of this study (Smith 1979; Bayliff 2002). However, considering the evidence for segregation in other *D. delphis* populations, this may be the more likely explanation for the observed age distribution than a non-stable age distribution of the population. The “dip” in animals less than two years may also be a sampling artifact, partially explained by limited sampling of these age classes by observers and calves that were initially present in the school but not caught in the purse-seine net (Archer et al. 2001).

Figure 22. Age distribution of female *D. delphis* in the N. Pacific. Data taken from Ferrero and Walker (1994).



The under representation of both calves and juveniles in the sample may be an artifact of selectivity and vulnerability issues associated with the fishery.

Length at birth

The mean of overlapping fetal and calf lengths likely underestimates the length at birth because of the greater number of fetuses at the lower and middle portion of the length range (Figure 12). This distribution may reflect perinatal mortality or age bias in sampling. Estimates of mean length at birth based on the SOFI and logistic methods are more likely positively biased since unobserved deaths of nursing calves have been documented for *S. attenuata* and *S. longirostris* impacted by the same fishery (Archer et al. 2001), and thus the sample is likely missing a proportion of calves.

A maximum difference of -3.4 cm in ELB occurred if 15% more calves (Archer et al.'s 2001 estimate of the maximum number missing) were added to the 75 cm length class. However, this was not significantly different from the original calculated ELB in this study ($P = 0.065$). The non-significant findings demonstrate that other parameter estimations that use ELB (e.g., growth curves and back-calculated birth dates) will not be significantly biased if the upper range of undocumented calf mortality does not exceed 15%.

Age, length, and sexual maturation

If juveniles are indeed “missing” from the sample as the comparison of a stable age distribution to that of this study suggests (Figure 10), the average ASM may be underestimated. For the purposes of estimating an alternative upper range of ASM, all “missing” animals less than 12 years are assumed to be immature animals (schooling elsewhere according to maturity status and thus not sampled).

If “missing” animals from the stable age distribution (Figure 10) were included in the logistic regression analysis, ASM was calculated as 10.2 years. (95% CI, 9.9 - 10.4), which is two years older than I calculated using the data available. This alternative estimate of ASM must be considered in population models of female central *D. delphis*.

A difference exists between the average ASM and mean age at first conception (0.7 years or 8.4 months), indicating that females do not conceive immediately following attainment of sexual maturity. Alternatively, it could be a result of the potential negative bias in the average ASM. In addition, the time between mean age of conception and mean age at first birth exceeds the gestation period by 4.3 months. This may indicate that perhaps some females may abort after first conception and become pregnant again, thus extending the time from first conception and first birth past the expected gestation time. These differences may exist because fertility and reproductive success are generally depressed in newly mature female cetaceans (Boyd et al. 1999).

The mean length of sexually mature females (195.2 cm) is comparable to previous mean adult length estimates of 194.3 cm (Perrin et al. 1985) and 194.8 cm (Perryman and Lynn 1993) for central *D. delphis* females.

Ovulation

The wide scatter in the plot of *corpora* on age for all individuals (Figure 16a) demonstrates the individual variation in ovulation rates that has also been documented in studies of other species (Perrin et al. 1976b; Perrin et al. 1977; Myrick et al. 1986). Individuals do not necessarily begin to ovulate at the same age and thus the slope of the regression of number of *corpora* on age class should

not be used as the average ovulation rate. The asymmetry of *corpora* scars in each ovary indicates that there is a prevalence of activity in the left ovary, similar to what has been found in other delphinids (Perrin et al. 1976a; Perrin et al. 1977).

Reproductive phases and calving interval

The observation that pregnancy rate decreases and lactation period increases with age (Figure 21) suggests that either younger females wean their calves earlier or do not successfully rear their calves, thus becoming pregnant more often than older females.

Lactation and resting phases and both estimates of calving interval are based on the assumption of no fetal mortality and are therefore minimum estimates. If central *D. delphis* experiences high fetal mortality rates similar to other ETP dolphins (Perrin et al. 2003), the observed proportion of pregnant females would be inflated by animals experiencing multiple re-impregnations following miscarriages. If fetal mortality were significant, calculated reproductive phases and calving intervals would be underestimates and APR overestimated because they are based simply on the proportion of pregnant females in the sample. Perrin et al. (2003) incorporated fetal mortality estimates to adjust the average calving interval of *S. attenuata* and *S. longirostris* from 3 to 5 years, and if true for *D. delphis*, calving intervals could be on average 1.7 times longer reported. However, if high rates of fetal mortality are a result of fishery interactions, this adjustment may be lower since *D. delphis* is less impacted by the tuna purse-seine fishery (Smith 1979; Hall 1998) than the species used in the fetal mortality study.

Comparison to N. Pacific population

Central *D. delphis* differ markedly in size from their conspecifics in the N. Pacific. Although born at similar lengths (one-sample *t*-test: $0.05 < P < 0.10$), central *D. delphis* are significantly longer at age two (159.4 cm vs. 146.4cm), LSM (185.9 cm vs. 170.7 cm) and mean maximum adult size (195.5 cm vs. 179.8 cm) (*t*-test: $P < 0.001$ for all comparisons). In order to compare maximum adult size to the N. Pacific study (Ferrero and Walker 1994), I calculated the average total body length of specimens greater than 16 years as described in Ferrero and Walker (1994) who did not report an asymptotic length predicted by a continuous growth curve. Average ASM was comparable between the two populations, indicating that central *D. delphis* grow faster, having to reach a greater size in the same amount of time. These observed differences, in combination with length differences in adult size noted within the ETP (Perrin et al. 1985; Perryman and Lynn 1993), indicate the existence of geographic variation in this species with longer individuals found in the tropics. Perhaps the productive waters of the Costa Rica Dome in the central region provide a stable rich prey source that allows *D. delphis* to reach a greater size.

The two-phase growth curve shows a marked secondary growth spurt for central *D. delphis* females, similar to those found in *S. longirostris* and *S. attenuata* and North Pacific *D. delphis* (Perrin et al. 1976a; Perrin et al. 1977; Ferrero and Walker 1994). Growth presumably slows after weaning as the calf learns to forage on its own, increases in preparation to attain a sufficient size for

reproductive maturity, and slows again as resources are put into reproductive activities and the animal nears asymptotic length.

Comparison to other delphinids in the ETP

S. l. orientalis, whitebelly spinners (a form of *S. longirostris*), and northeastern offshore *S. attenuata* inhabit the same general geographic area as central *D. delphis*. Out of these three closely related species, *D. delphis* appear to be most similar to *S. attenuata* in life history parameters associated with length: ELB, LSM, and asymptotic length (Table 13). However, central *D. delphis* reach sexual maturity at a significantly earlier age (one sample *t*-test: $P < 0.0001$) and have a calving interval that is one year shorter than that of northern *S. attenuata*. These differences impart reflect differences in longevity between the two species: *S. attenuata* live longer (38 years; (Myrick et al. 1986) than *D. delphis* (25 years). *S. attenuata* also grow slower during their first year (3.13 cm /month (Hohn and Hammond 1983) vs. 4.1 cm/month), and this trend of slower growth (typical of longer-lived animals) likely continues, therefore taking them more time to reach sexual maturity.

Central *D. delphis* have a shorter calving interval than the other ETP small delphinid species previously mentioned, and so this trait may be reflect a unique life history characteristic that has evolved in this species and is not related to longevity (longevity of spinners is similar to *D. delphis*; Table 13). This shorter calving interval likely results from the greater number of females that lactate while they are pregnant: 26.8% vs. 9.3% in spotted (Myrick et al. 1986), 2.5% in *S. l. orientalis*, and 5.5% in whitebelly spinners (Henderson et al. 1980). Two

Table 13. Comparison of life history parameters between northern offshore pantropical spotted, eastern spinner, whitebelly spinner, and common dolphins. Reference providing data indicated by letter. ELB = estimated length at birth, LSM = length at attainment of sexual maturity, ASM = age at attainment of sexual maturity, APR = annual pregnancy rate.

Species	ELB	1st yr Growth (cm/month)	LSM	ASM	Asymptotic length (cm)	Calving	% of lactating females that are pregnant	Calving Interval (years) (1/APR)	APR	Maximum reported age (years)
Northern offshore spotted	85.4 (f)	3.13 (f)	181 (a)	11.3 (g)	190 (a)	Spring/Autumn (e)	9.3 (g)	3.03 (g)	0.33 (g)	38 (g)
Eastern spinner	77 (b)	4.75 (b)	164.1 (b)	5.5 (b)	170.9 (b)	March-June (e)	1.43 (b)	2.95 (c)	0.34 (c)	26 (j)
N. whitebelly spinner	75.9 (d)	4.3 (d)	168.8 (d)	7.1 (d)	174.9 (d)	Spring/Autumn (e)	5.5 (c)	2.8 (d)	0.36 (d)	23 (d)
<i>D. delphis</i> (N. Pacific)	82 (h)	N/A	170.7 (h)	8 (h)	179.4 (h)	May-June (h)	N/A	N/A	N/A	27 (h)
<i>D. delphis</i> (ETP)	85.2 (i)	4.1 (i)	185.8 (i)	8.1 (i)	196.5 (i)	all year (i)	26.8 (i)	2.16 (i)	0.47 (i)	25 (i)

a = Perrin et al. (1976), b = Perrin et al. (1977), c = Henderson et al. (1980), d = Perrin and Henderson (1984), e = Barlow (1984), f = Hohn and Hammond (1985), g = Myrick et al. (1986), h = Ferrero and Walker (1995), i = this study, j = Chivers (2002)

possible explanations for the occurrence of more simultaneously lactating and pregnant females may be because they are either (a) compensatory in reproductive output in response to a reduction in population abundance due to fishery mortality, or (b) better able to manage the increased energy demands of lactating while pregnant since they inhabit upwelling modified regions in the ETP (Au and Perryman 1985; Fiedler and Reilly 1994). The productive waters of these upwelling regions likely support an abundant prey source of deep scattering layer organisms that *D. delphis* feed on (Osnes-Erie 1999). These upwelling regions may provide a richer food source than the less productive Tropical Surface Water that *S. longirostris* and *S. attenuata* inhabit.

Although an increase in simultaneously pregnant and lactating females has been hypothesized as a mechanism to increase reproductive output in response to incidental mortality in *S. attenuata* (Chivers and Myrick 1993), the more likely hypothesis is (b) because *D. delphis* is the least exploited species out of those discussed previously and thus would not necessarily be expected to exhibit a density compensatory response. However, it is also possible that both a decreased calving interval and lactating while pregnant may produce in *D. delphis* a higher intrinsic reproductive rate, which could be an adaptation for rapid population growth in response to some ecological or evolutionary pressures.

The lack of reproductive seasonality in central female *D. delphis* is unique, considering that *Stenella* spp. inhabiting the ETP reproduce seasonally (although for some species it is diffuse; Barlow 1984), as do *D. delphis* in the N. Pacific (Ferrero and Walker 1994). The difference in seasonality between *D.*

delphis in the N. Pacific and in the ETP may simply demonstrate a latitudinal gradient in reproduction in response to different environments: temperate versus tropical. Seasons of high productivity are brief at higher latitudes and more protracted at lower latitudes, therefore timing in reproduction is highly synchronized in high latitude populations and more diffuse at low latitudes (Bronson 1989; Boyd et al. 1999). However, what accounts for the difference between *D. delphis* and the *Stenella* spp. inhabiting the same latitudinal gradient? The distributions of *Stenella* spp. in the ETP are known to change seasonally while that of *D. delphis* does not (Reilly 1990). This suggests that the upwelling modified regions that *D. delphis* inhabit may provide an environment that is more stable throughout the year in terms of environmental parameters, food availability, and predation risk, all factors that typically affect movement patterns. Females could exploit this stability and meet the energetic demands of pregnancy and lactation year-round.

Conclusions

Comparisons

Differences between central *D. delphis* and those in the N. Pacific indicate that large-scale geographic variation in life history occurs for this species. This is likely a reflection of the tropical and temperate environments that these populations inhabit, respectively. Differences between central female *D. delphis* and *Stenella* spp. inhabiting the same geographic region may also reflect adaptations to different habitats. The upwelling modified tropical waters in which central *D. delphis* live sharply contrasts with the surrounding warm, less

productive Tropical Surface Water that *S. attenuata* and *S. longirostris* inhabit (Au and Perryman 1985).

Management

Management strategies for populations subject to exploitation often use estimated rates of increase in population size that are based on vital rates. Reilly and Barlow (1986) found that out of four vital rates examined, delphinid population rates of increase were most sensitive to calving interval and non-calf survival rate, followed by age at first birth, and were insensitive to changes in calf survival rate. If calving interval was increased by one year, population rates of increase were found to decrease by approximately 2%. Under this example, rates of increase in central female *D. delphis* population size would be higher (due to their shorter calving interval) than *S. attenuata* and *S. longirostris*. This would enable the central *D. delphis* population to recover from fishery exploitation (or some other mortality event) more quickly than the *Stenella* spp. Expected recovery rates can be modeled using the reproductive parameters, such as calving interval and ASM, estimated in this study.

Summary

Central female *D. delphis* are born at approximately 85.2 cm. They attain sexual maturity at an average age and length of 8.1 years and 185.9 cm, respectively. Calving occurs throughout the year, approximately every 2.5 years after a gestation of 11.3 months, a lactation period of 16.1 months and a resting period of 2.9 months. A high percentage (26.8%) of lactating females are simultaneously pregnant, allowing some females to shorten their calving interval. Females live to at least 25 years and evidence of senescent females was not found.

Several caveats to traditional parameter estimations were discussed with alternative estimates presented for ELB, ASM, and calving interval. These alternative estimates need to be considered if these parameters are to be used in population models of *D. delphis* in the ETP.

CHAPTER 5: SPATIAL AND TEMPORAL VARIABILITY IN TOTAL BODY LENGTH, AGE, AND BREEDING SEASONALITY OF FEMALES

Introduction

The central stock of *D. delphis* inhabits a large area within the ETP that extends from near shore to thousands of miles offshore. Concentrations of *D. delphis* are found here in upwelling modified regions, with cool surface temperature and a shallow, weak thermocline (Fiedler and Reilly 1994). The primary upwelling modified region that dominates the water they inhabit is the Costa Rica Dome (Figure 2). This thermocline dome has a distinctly higher plankton biomass than surrounding tropical waters and changes seasonally in structure and location (Fiedler 2002a). Although *D. delphis* habitat quality is highest at the Costa Rica Dome (Fiedler and Reilly 1994), animals live in surrounding areas as well. The distance between and/or varied degrees of upwelling modified habitats within this region could potentially drive fine scale population structure within the central stock that might be apparent through differences in life history parameters.

Life history parameters have been shown to vary between neighboring stocks of other delphinids in the ETP (Barlow 1985; Hohn and Hammond 1985; Perrin et al. 1985; Chivers and Myrick 1993). For example, *S. l. orientalis* and northern whitebelly spinner dolphins (a form of *S. longirostris* in the ETP) were found to vary in total body length, breeding seasonality, and ovulation rates (Perrin et al. 1985), whereas northern and southern stocks of *S. attenuata* were found to differ in total body length, average LSM, proportion pregnant (Barlow

1985), and the average ASM (Chivers and Myrick 1993). However, interpretation of these differences is not straightforward because these populations experienced varying degrees of mortality in the yellowfin tuna purse-seine fishery and may be exhibiting not only inherent population differences but also varying degrees of density compensatory responses.

Incorporating both spatial and temporal analyses of life history parameters together may aid in interpreting and hypothesizing causes of observed results. However, these two elements have not been fully incorporated in the past. Temporal trends in reproductive parameters have been examined separately for northern and southern offshore *S. attenuata*, *S. l. orientalis* and whitebelly spinner dolphins, and central *D. delphis* (Barlow 1985; Hohn and Hammond 1985; Chivers and Myrick 1993; Chivers and DeMaster 1994). These studies focused on detecting density compensatory responses and sampling biases related to the tuna purse-seine fishery. However, Chivers and Myrick (1993) did not observe predicted compensatory responses and suggested that they might not have been detected due to biological differences between subpopulations or environmental periodicity. However, these hypotheses were not tested.

This chapter explores differences between potential subpopulations within central *D. delphis* and the environment they live in, over time. *A priori* groups of central *D. delphis* are defined based on oceanographic variables, distance from shore, and distance between similar habitats. Using these *a priori* groups, mature female total body length, age, and calving season are used as proxies to determine

whether oceanography may be driving fine scale population structure and whether these parameters have changed over time.

Methods

Defining *a priori* groups

Oceanographic parameters and distance from shore were examined as variables to define *a priori* spatial groupings within central *D. delphis*. Mean thermocline (THERM) and 20 °C isotherm depth (Z20), SST, and surface chlorophyll concentration (CHL) were extracted by Fiedler and Talley (2004; In press) from the World Ocean Database. Data files from 1950 through those updated as of 30 August 2003 were used. The 20 °C isotherm has been used as an index of thermocline depth in the tropics (Hansen and Herman 1988; Kessler 1990) and has been used in conjunction with other oceanographic variables to characterize *D. delphis* habitat in the ETP (Reilly 1990; Reilly and Fiedler 1994; Reilly et al. 2002). Although it is only an approximation, I have used the 20 °C isotherm depth as a comparison and complement to actual thermocline depth, defined as the depth at which the greatest temperature change occurs, because of its historical significance. Oceanographic variables were averaged within one-degree map blocks and associated with the sampling locations of individual dolphins. Distance from shore (DIST) was also used as a possible discriminating variable because several studies have shown that morphometric differences exist between some offshore and inshore populations of delphinids (Walker 1981; Douglas et al. 1984; Perrin et al. 1985). Square root transformations of THERM and DIST, and a log transformation of CHL were performed to improve the normality of their distributions.

The relationship of oceanographic variables and distance from shore to total length of mature females and to each other was examined using a Spearman rank correlation test to determine which variables to include in the principal component analysis (PCA). The variables $Z20$, \sqrt{THERM} , and SST were used in a PCA as descriptors of the habitat. These variables were used because the quality of ordination in a PCA is dependent on the collinearity of variables. Although CHL has been used in previous habitat analyses (Reilly and Fiedler 1994; Reilly et al. 2002), it was not used in this PCA because (1) it was not correlated with total body length and (2) it was negatively correlated with all other oceanographic variables. A negative correlation between variables could have caused the PCA to contribute more loading to this difference rather than to the covariation of the other variables. DIST was also excluded from the PCA because it was not correlated with total body length. The standardized score from the PCA (Table 14) was used in a k -means cluster analysis of collected samples.

A two-group k -means cluster analysis was used to separate central *D. delphis* into groups based on habitat differences reflected by the PCA scores described above. *A priori* groups for life history analyses were formed based on these results.

Temporal and spatial comparisons

Sample frequencies for each hypothesized population were examined to determine whether sampling biases existed over time and/or season. Assignment to season was based on the phases of the Costa Rica Dome. The following stages

Table 14. Results of PCA. Component loadings and percent total variance values indicate that data structure was effectively summarized by all variables used.

Variable	Eigenvectors	Component loadings
Z20	0.587	0.962
\sqrt{THERM}	0.585	0.957
SST	0.560	0.916
Latent roots (Eigenvalues)		
1	2	3
2.680	0.234	0.086
Percent of total variance explained: 89.341		

of the Dome (Fiedler 2002a) were used to define “seasons” for my analysis: (1) coastal shoaling (February-April), (2) separation from the coast (May- June), (3) countercurrent thermocline ridging /intensification and expansion to the west (July-November), and (4) deepening (December-January).

The distribution of samples was heavily skewed towards the early years (1973-1979) of this study, with another peak in sampling in 1988 and 1989 (Figure 23). This bias made comparison across all years inappropriate. Initially, two time periods, 1976-1977 and 1988-1989, were selected as proxies for “early” and “later” years to investigate temporal variation. These time periods were chosen based on their large sample sizes and similarity in distribution of samples across habitat groups (Figure 23). However, the “season” when samples were collected was different between these two time periods. During 1976-1977 most samples were collected during the “intensification and expansion west” phase of the dome, whereas in 1988-1989 samples were largely collected during the “coastal shoaling phase” of the dome (Figure 24a). Therefore, to compare samples collected in the same season, I selected a slightly earlier time period for the analyses to reduce the influence of animal movement due to season. In 1973-1974, the majority of samples were collected during the coastal shoaling phase (Figure 24b), and so this became my “early” time period.

Mean length and age of sexually mature females was compared between *a priori* groups and time periods, using a two-way ANOVA. Seasonality in female reproduction was examined using the Kuiper’s test on back-calculated birth dates,

Figure 23. Distribution of central female samples for each *a priori* group, across years. Group A = individuals north of the Costa Rica Dome, Group B = individuals sampled “on” the Costa Rica Dome, Group C = individuals south of the Costa Rica Dome.

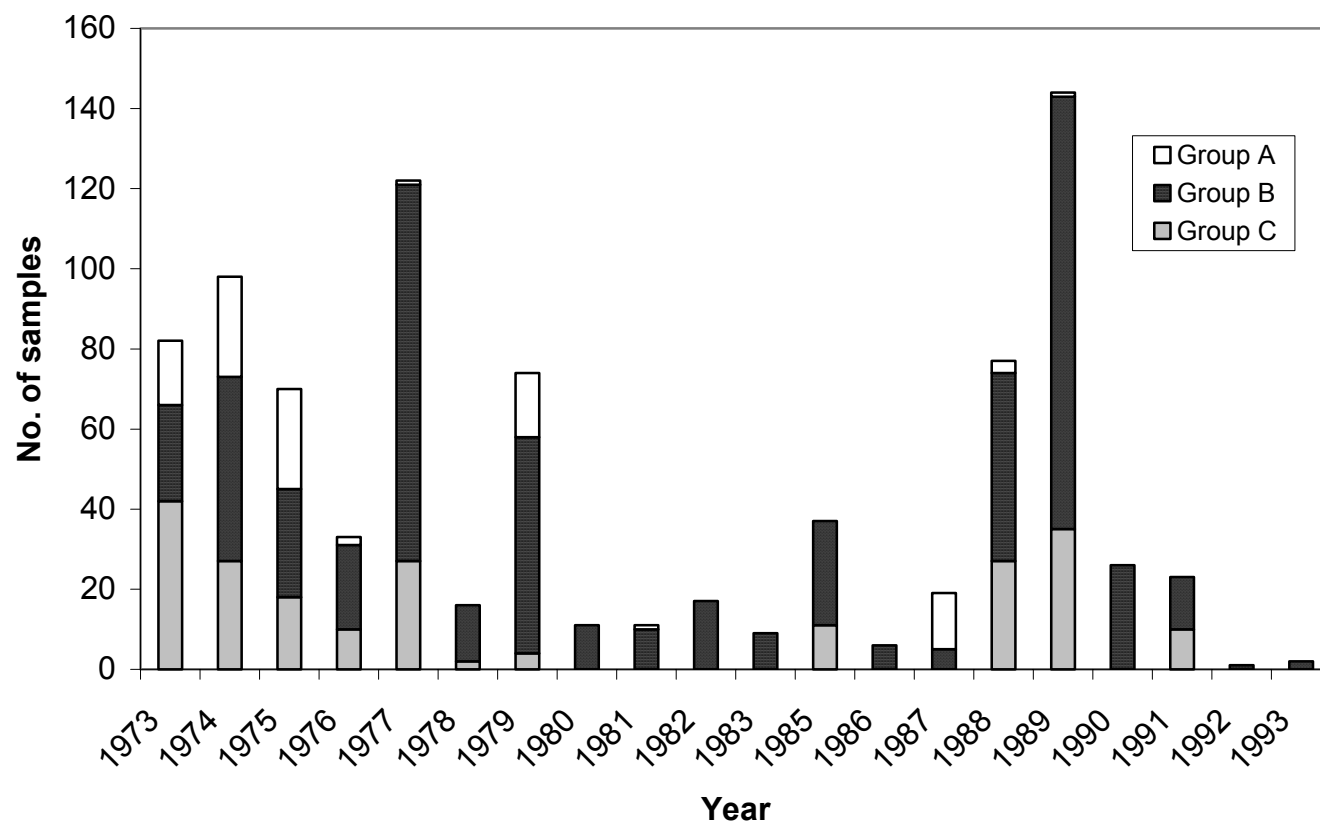
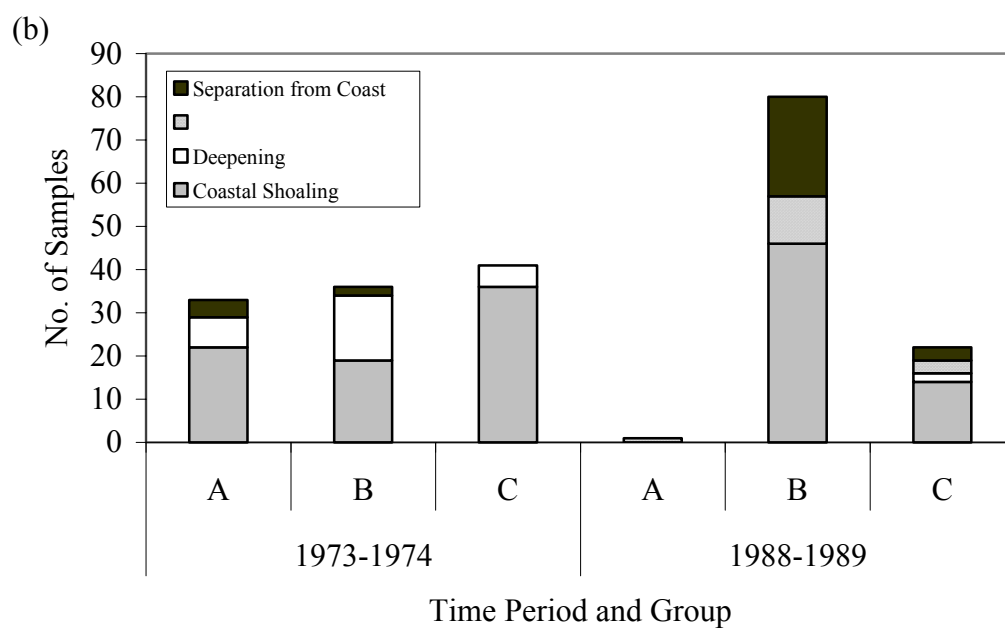
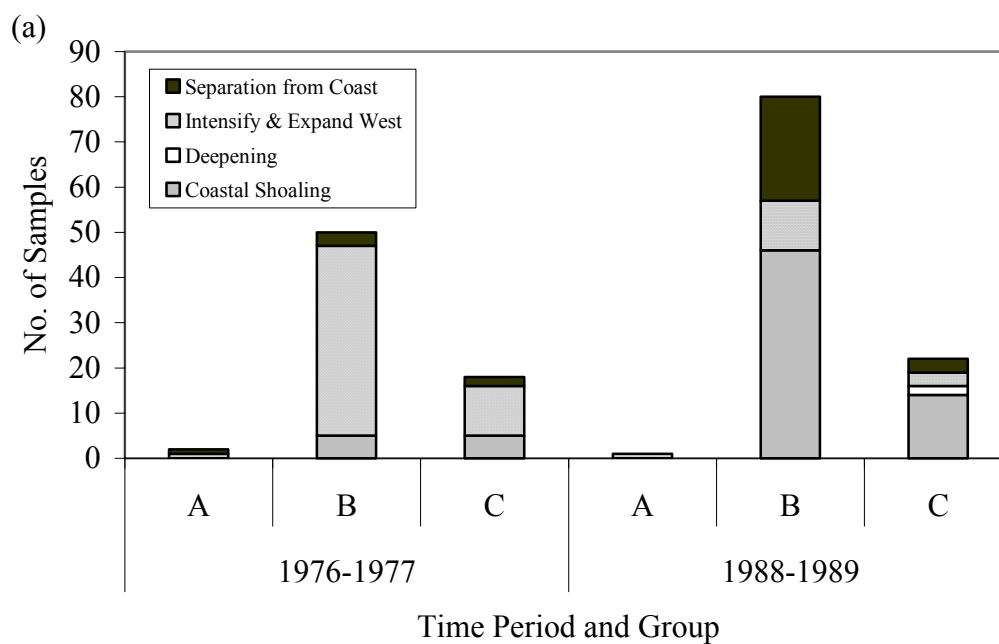


Figure 24. Distribution of samples across dome season, for each *a priori* group and time period. Group A = individuals north of the Costa Rica Dome, Group B = individuals sampled “on” the Costa Rica Dome, Group C = individuals south of the Costa Rica Dome.



as described in Chapter 4. Due to limited sample sizes, a comparison of seasonality in reproduction between time periods was not possible.

Results

A priori groups

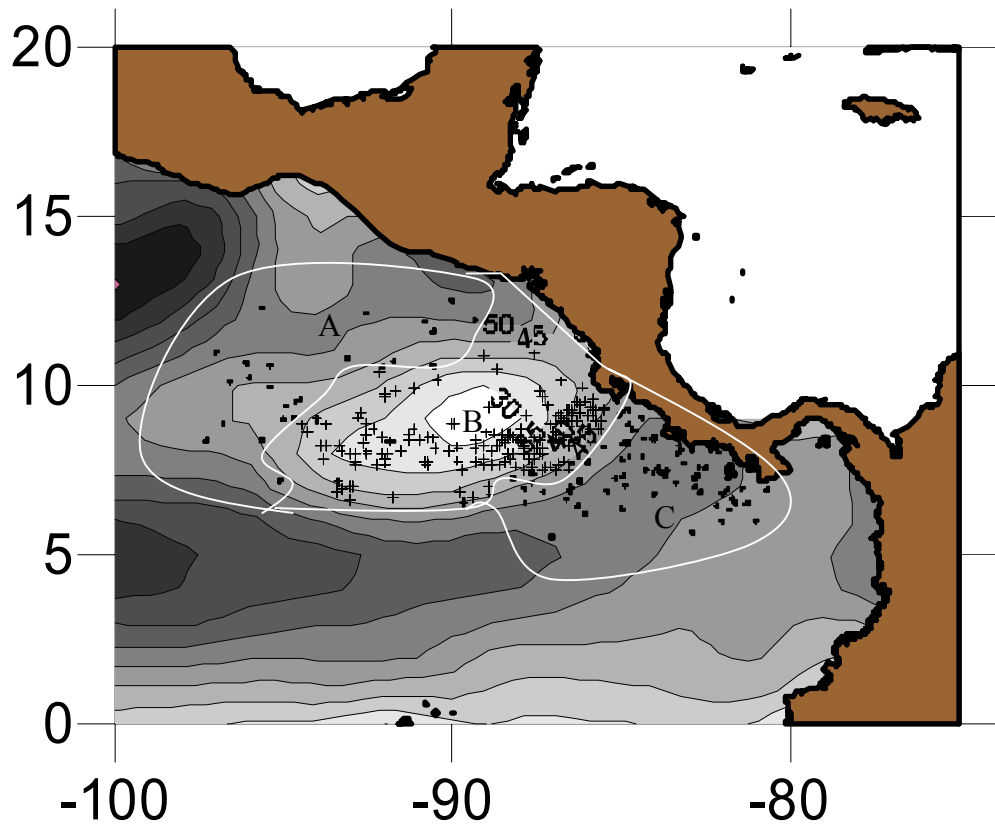
The variables Z20 ($P = 0.0066$), THERM ($P = 0.0014$), and SST ($P < 0.0001$) were all significantly correlated to total length of mature females, as well as being correlated with each other (Table 15). DIST ($P = 0.5329$) and CHL ($P = 0.3690$) were not correlated with total length. Component loadings indicate that in descending order, Z20, \sqrt{THERM} , and SST contributed significantly (Tabachnik and Fidell 1989) to the principle component structure (Table 14). The high total variance explained (89.341 %) indicates that the data structure was effectively summarized in a few dimensions.

The two-group *k*-means cluster analysis identifies two oceanographic habitats, which separate the samples into “on” and “off” the Costa Rica dome (Figure 25), an oceanographic feature typically identified by the doming of the isotherms. Although the farthest southeast and northwest groups are considered to be in the same habitat group for both *k*-means analyses, these will be considered separate groups. The distance separating these groups (a minimum of 300 nmi) likely prevents frequent intermixing between them because they are on either side of the Dome and so they are treated separately here. In summary, three *a priori* groups for the spatial analysis are considered and identified as A, B, and C (Figure 25). Groups A and C are considered “off” the Dome habitat, representing the northern and southern most groups of central *D. delphis*, respectively. Group B is the “on” the Dome habitat group.

Table 15. Spearman rank correlations of oceanographic variables, distance from shore, and total length of mature females. Z20 = 20 °C isotherm depth, SST = sea surface temperature, LOGCHL = log (chlorophyll conc.), DIST = distance from shore.

Variable	by Variable	Spearman ρ	Prob > $ \rho $
Z20	TOTLENGTH	0.1266	0.0066
SST	TOTLENGTH	0.2100	< .0001
SST	Z20	0.7577	< .0001
LOGCHL	TOTLENGTH	0.0420	0.3690
LOGCHL	Z20	-0.4181	< .0001
LOGCHL	SST	-0.0712	0.1279
$\sqrt{\text{DIST}}$	TOTLENGTH	-0.0292	0.5329
$\sqrt{\text{DIST}}$	Z20	-0.4219	< .0001
$\sqrt{\text{DIST}}$	SST	-0.0888	0.0572
$\sqrt{\text{DIST}}$	LOGCHLOR	0.2546	< .0001
$\sqrt{\text{THERM}}$	TOTLENGTH	0.1485	0.0014
$\sqrt{\text{THERM}}$	Z20	0.9169	< .0001
$\sqrt{\text{THERM}}$	SST	0.8150	< .0001
$\sqrt{\text{THERM}}$	LOGCHLOR	-0.2360	< .0001
$\sqrt{\text{THERM}}$	$\sqrt{\text{DIST}}$	-0.1033	0.0269

Figure 25. Separation of central *D. delphis* females based on two-group *k*-means cluster analyses. Symbols represent groupings based on *k*-means cluster analyses and outlined areas represent groups defined by cluster analyses and distance of groups from each other. Contours represent 20 °C isotherm depth (m).



A shallow thermocline depth, lower SST, and higher chlorophyll concentration characterizes the habitat of group B that is centered on the Costa Rica dome (Table 16) compared to groups A and C. The thermocline depth and SST increases while CHL decreases from “on” the Dome to “off” the Dome (i.e., groups A & C, Table 16). Comparatively, group A extends on average, farthest from shore, followed by group B and then group C.

Temporal and spatial comparisons

Samples from group A were largely collected from 1973-1975, and thus once data were limited to two time periods, group A sample sizes were too small for temporal comparison. Although three *a priori* groups were defined, only groups B and C will be compared due to sample size limitations.

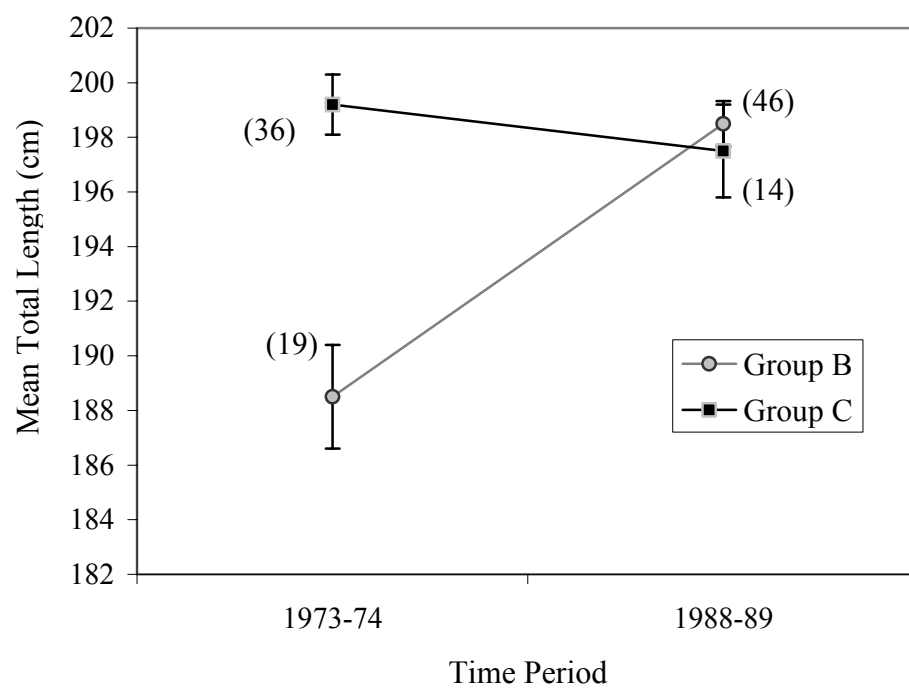
Mean total body length of mature females varied both spatially and temporally. Two-way ANOVA results show a significant difference between time periods ($F_{1,114} = 9.619$, $P = 0.0024$) and groups ($F_{1,114} = 13.093$, $P = 0.0004$), with interaction effects ($F_{1,114} = 19.034$, $P < 0.0001$). The Tukey Multiple Comparison Test demonstrated significant differences ($P < 0.05$) in total length for group B between time periods and between groups B and C during 1973-74. Examination of the interaction plot (Figure 26) indicates that group B was 10 cm shorter than C in the “early” years and that population B increased in length over time while group C did not, leading to undetectable differences between the two groups in the “later” years.

Mean age of mature females did not vary over time or space. Two-way ANOVA results indicated that there was no significant difference between time periods ($F_{1,79} = 2.5875$, $P = 0.1119$), groups ($F_{1,79} = 0.3499$, $P = 0.5559$), or

Table 16. Mean values of variables associated with *a priori* groups. Groups A and C represent areas “off” the dome whereas group B represents the “on” dome habitat.

Group	Thermocline depth (m)	20 °C Isotherm depth (m)	Chlorophyll (mg/m ³)	SST (°C)	Distance from shore (nmi)
A	41.7	47.2	0.361	27.9	273.0
B	29.7	36.3	0.400	27.3	216.1
C	38.8	49.8	0.259	27.9	86.4

Figure 26. Interaction plot of mean total length with time period and group membership. Numbers in parentheses indicate sample size; error bars represent standard error of the mean.



interactions between group and time ($F_{1,79} = 1.6863$, $P = 0.1980$). Back-calculated birth dates were not significantly different from a uniform distribution for both groups B ($K = 0.75$, $P > 0.10$) and C ($K = 0.30$, $P > 0.10$), indicating no difference in seasonality of female reproduction (Figure 27).

Discussion

A priori groups

Stratifying data according to oceanographic variables through the use of PCA and *k*-means cluster analysis provided a framework for spatial comparisons based on habitat. The application could easily be extended for comparing genetic, morphometric, and life history characteristics of other marine species that inhabit diverse oceanographic regions. This method could be used for developing *a priori* groups for developing potential stock designations if animals occur in oceanographic regions that could effectively limit animal movement.

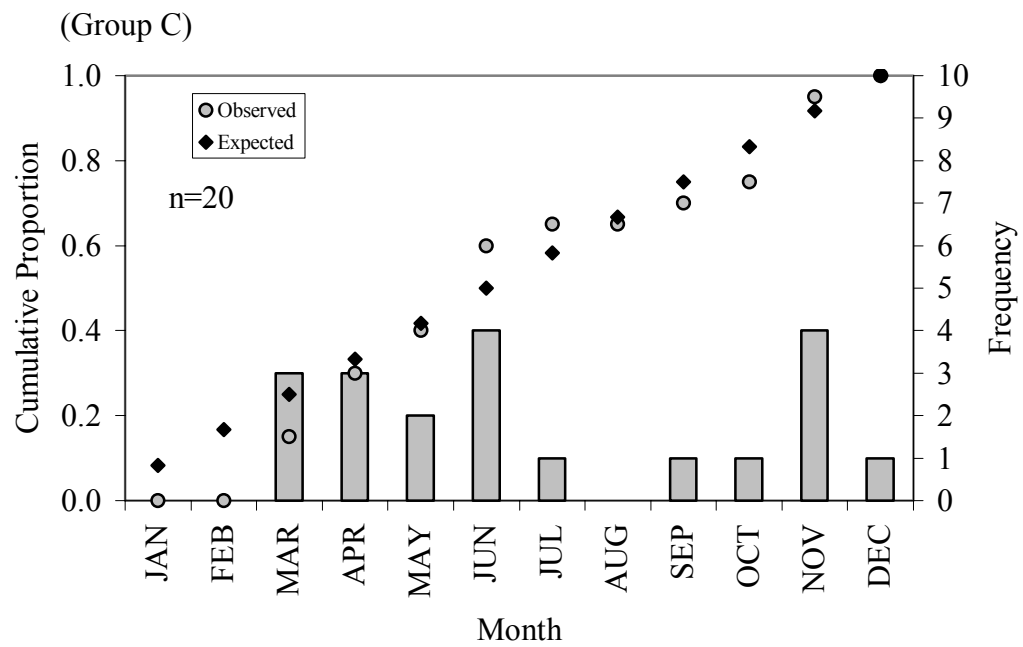
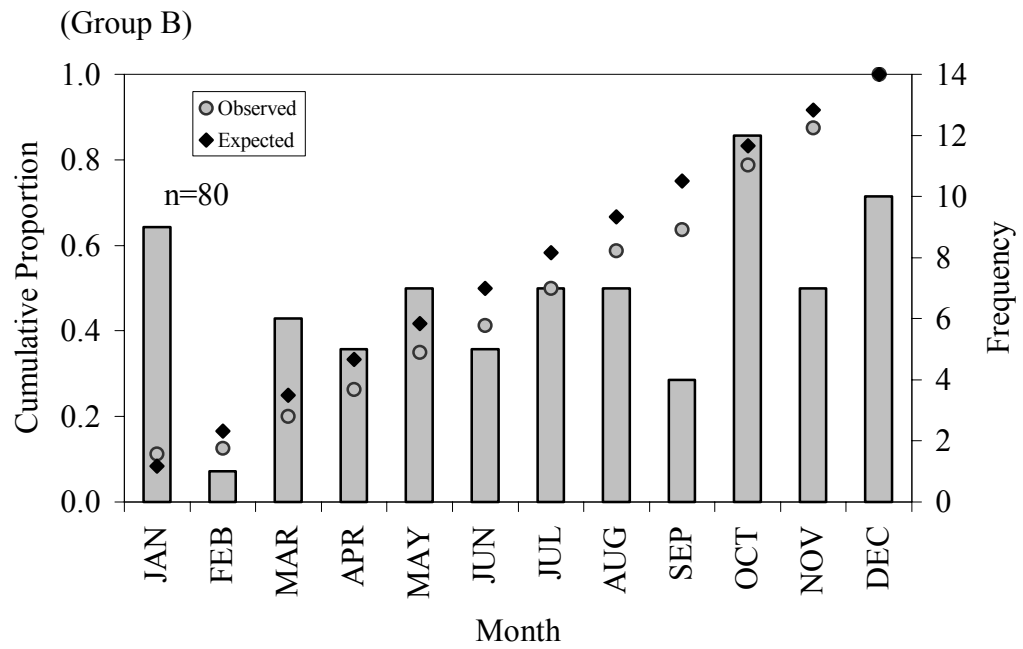
Alternatively, it could be used for developing finer scale strata for examining clinal differences by increasing the number of groups specified in the *k*-means cluster analysis.

Spatial and temporal comparisons

Why sexually mature females in group B were different in total length from group C in the “early” years and total length in group B mature females changed over time cannot be determined. However, three hypotheses could explain the differences: (1) movement of animals due to environmental changes, (2) morphological change in response to environmental changes, and (3) sampling biases.

Figure 27. Back-projected birth date distributions for groups B and C.

Cumulative back-projected birth date distributions are not significantly different from a uniform cumulative distribution for groups B and C. Bars indicate frequency of birth dates; points indicate observed and expected cumulative proportions.



Movement of animals due to environmental change

Groups B and C could be distinct subpopulations within central *D. delphis*, and the apparent increase in length over time of group B may be due to movement of the longer group C animals into their habitat. In fact, a decrease in the abundance of the northern stock of *D. delphis* in the ETP and a concomitant increase off southern California, starting in the late 1970s, suggests a large-scale shift in the distribution of *D. delphis* may have occurred in the eastern North Pacific (Anganuzzi and Buckland 1994). During the time of this hypothesized shift in distribution, a cool to warm oceanographic regime shift occurred in the North Pacific during the winter of 1976-77. These changes were also apparent, although to a lesser degree, in the warm pool area of the ETP, where central *D. delphis* occur (Fiedler 2002b). This regime shift could have prompted a shift in distribution of *D. delphis* within the region. Either group C animals replaced group B as these animals moved elsewhere, or group C animals mixed with group B, melding the once distinct subpopulations into one.

Another possibility is that sampling in the “early” years captured a temporary distributional shift within the ETP of shorter animals from the northern ($\bar{X} = 178.5; 179.2$ cm; (Perrin et al. 1985; Perryman and Lynn 1993)) or southern ($\bar{X} = 188.5; 184.3$ cm; (Perrin et al. 1985; Perryman and Lynn 1993)) stocks in response to the 1972-73 El Niño-Southern Oscillation (ENSO). This is a reasonable hypothesis because *D. delphis* have been documented to shift their distribution interannually in response to ENSO events in the ETP (Reilly and Fiedler 1994). This shift likely occurs when the warm surface waters and deep

thermoclines associated with ENSO (Fiedler 2002b) reduce the habitat quality for *D. delphis*. This hypothesis implies that groups B and C were not different in average total length and that the observed difference may be an artifact of sampling different *D. delphis* stocks during ENSO. The relative distance between group B and the southern *D. delphis* stock is less than that between group B and the northern stock (Figure 28), suggesting that movement of southern rather than the northern stock animals into central stock habitat is more likely.

Although the roughly 240 nmi separating the southern stock and group B of the central stock may seem like a lengthy distance to travel, a radio-tagged *D. delphis* in the northeastern Pacific was documented traveling 270 nmi from its capture site (Evans 1975). Not only have *D. delphis* been documented traveling similar distances, but a shift in distribution greater than that proposed above was observed in 1987. Reilly and Fiedler (1994) reported that southern *D. delphis* only occurred in the far east off South America during the ENSO of 1987, whereas in La Niña conditions their range extended out to 110° W. If “far east” is assumed to be 85° W, then the distance that animals may have traveled between these distributions is roughly 1500 nmi. Using thermocline depth as an index of *D. delphis* upwelling habitat, during ENSO favorable conditions contracted eastward and southward at the equator and changed very little at the Costa Rica Dome (Figure 29). Thus, it is quite likely that individuals from the northern or southern stocks of *D. delphis* might travel to the area of the Costa Rica Dome in search of favorable conditions during ENSO.

Figure 28. Relative distance (indicated by arrows) between the northern and southern stocks and group C of the central stock. Data points are *D. delphis* sightings from SWFSC cruises. Lines surrounding data points indicate the management units to which these sightings would belong.

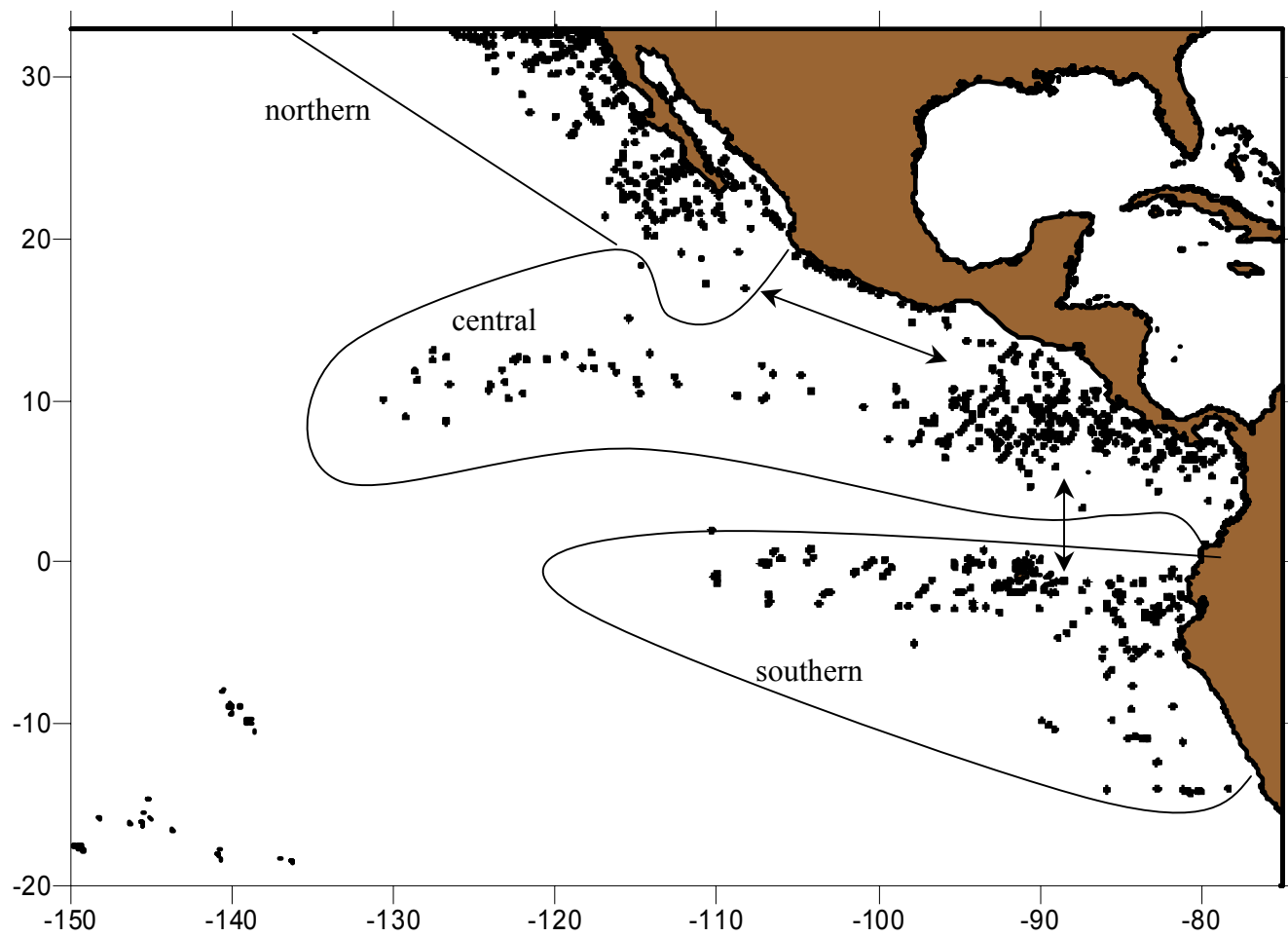
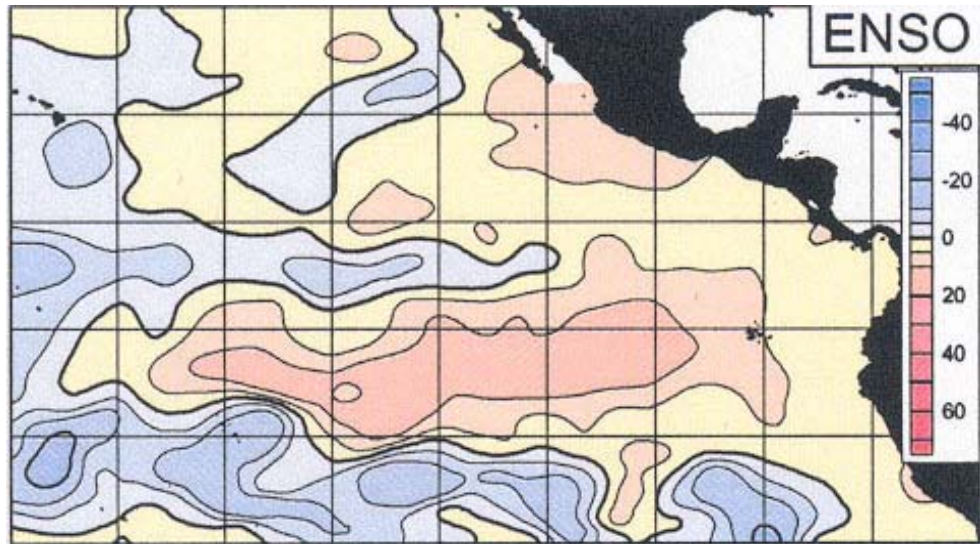


Figure 29. ENSO effect on thermocline depth ($-2 \times$ linear fit to Southern Oscillation Index). Orange and blue areas indicate deepening and shoaling of the thermocline, respectively. Figure taken from Fiedler and Talley (in press).



Morphological change in response to environmental change

If a shift in distribution did not occur, another hypothesis is that the observed change in total length for group B stemmed from a change in habitat and prey type and availability. The notion that length changed during such a short time period as the 1972-1973 ENSO is biologically impossible. A change in total body length over time, in response to a regime shift, is more of a possibility.

However, why would group C and not group B change? The only explanation for this would be if the habitat of group B changed and that of group C did not. To examine this possibility, the distribution of surface chlorophyll change between pre-and post-regime shift years in the study area was inspected. Groups B and C both inhabited areas of zero and positive chlorophyll change (Figure 30).

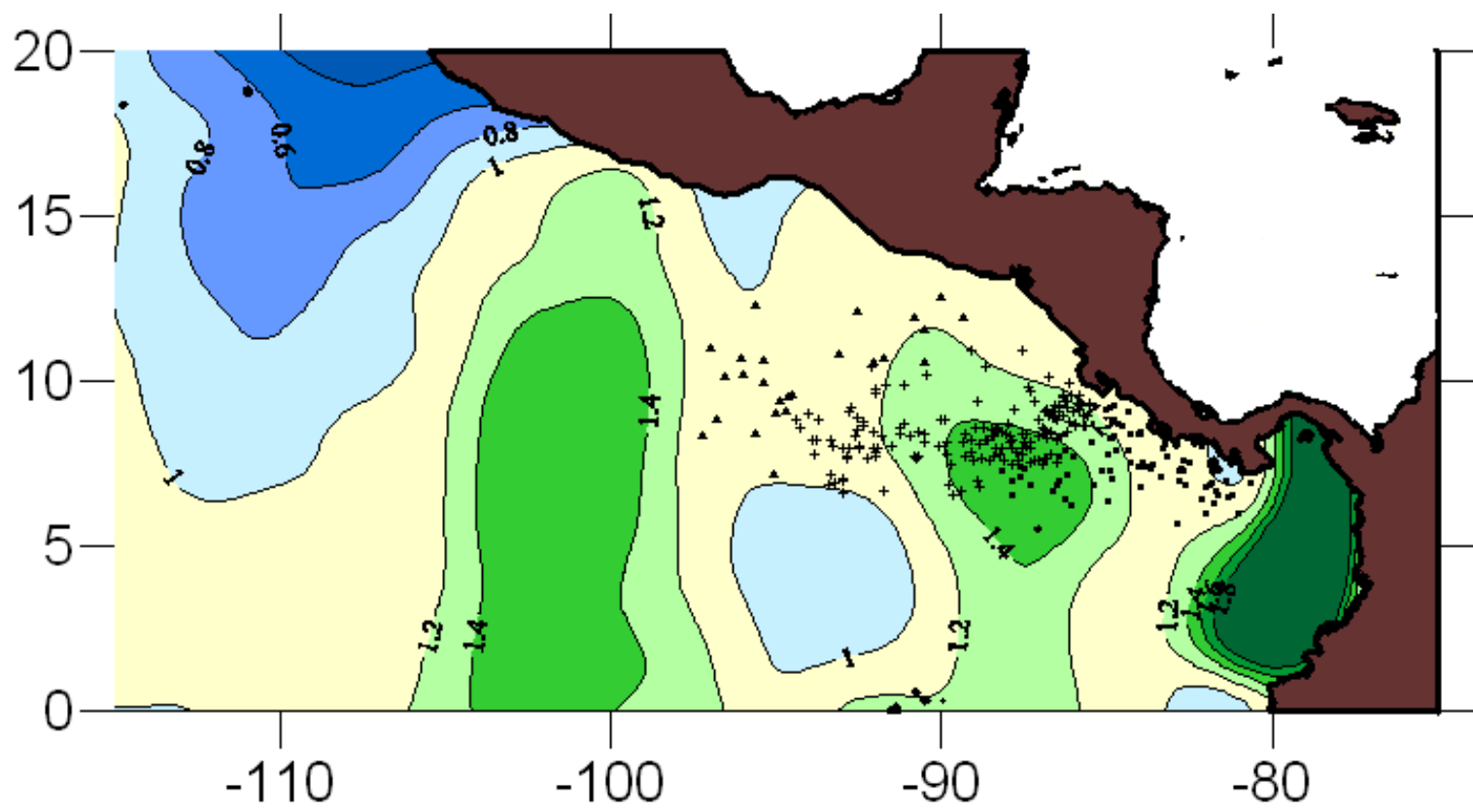
Considering that spatial and seasonal sampling differences between pre- and post-regime periods in the chlorophyll data exist and inconclusive spatial patterns in chlorophyll change were found, the above explanation seems unlikely.

Sampling biases

Potential sampling biases associated with by-caught dolphins in the tuna purse-seine fishery in the ETP abound and have been discussed in several papers (Perrin et al. 1976a; Barlow 1985; Perrin et al. 1985; Chivers and Myrick 1993; Archer et al. 2001). Three potential biases that were not removed through data stratification and their relation to this study will be discussed here: sampling methods, age structure, and number of dolphins killed per set.

Sampling protocol remained constant during the years of this study (1973-1993). The only difference in sampling design was that in 1973 vessel

Figure 30. Mean surface chlorophyll change (mg/m^3) between pre- and post-regime shift years (1980-1999)/(1955-1975). Symbols represent *a priori* group samples. Green coloration indicates positive change, yellow indicates no change, and blue indicates negative change in post-regime years. Darker colors indicate greater change. Chlorophyll data courtesy of Paul Fiedler, SWFSC.



Participation in the tuna observer program was voluntary, whereas starting in 1974 it was mandatory (Barlow 1985). Length and age measures are not likely to be effected by random vs. non-random vessel participation. Changes in the way total body length measurements were taken would be the only potential sampling protocol factor to bias the results of this study and there is no evidence of change in methods or equipment.

Perrin et al. (1985) addressed the possibility that differences in body length may be biased by differences in age structure (i.e., sampling young mature females would result in smaller mean lengths), but the mean age of mature females is constant across groups and time periods in this study and therefore not a likely source of bias to explain the differences in length found in this study. Another potential source of bias is the number of dolphins killed per set. The proportion of mature female northern *S. attenuata* was found to depend significantly on this variable (Barlow 1985). Barlow suggested that this association may be due to animals segregating by reproductive maturity and that vulnerability to high kill-per-set varies by maturity status. According to this rationale, parameters associated with only mature females would not be impacted by this bias, and therefore would not be of concern in this study.

The most likely explanation for the observed differences in length over time and space is that of a temporary shift in distribution during the ENSO of 1972-73. If this is the case, there is no evidence for additional subpopulations within central *D. delphis*. The lack of seasonality in both groups also supports this. However, the existence of subpopulations has not been disproved. Potential

biases and data stratification led to small sample sizes that inhibited exploring the data further. If samples become available in future years, further examination of life history data as well as genetic markers between the hypothesized populations A, B, and C would still be merited, considering the dynamic oceanography within this region.

If in fact there is movement between *D. delphis* stocks during ENSO events, there are implications for the stocks themselves and for estimates of growth and reproduction for central *D. delphis*. Mixing of stocks during ENSO events could increase the genetic diversity of the respective populations as well as provide potential colonists to central *D. delphis*. If a severe reduction in population abundance occurred, these colonists could make the central stock more resilient to such disturbances. However, movement of animals between stock boundaries also brings into question the meaning of “stock”. Is there gene flow between *D. delphis* stocks during ENSO and is it large and frequent enough to negate their stock designations that were based on the idea that they are reproductively isolated? Genetic markers for all three stocks need to be looked at in addition to examining the life history of the northern and southern stocks to determine whether they are maintaining a large degree of reproductive isolation.

Estimates of growth and reproduction of central *D. delphis* such as ELB, LSM, and dates of births (Chapter 4) would effectively be averaged by the inclusion of shorter animals from the northern or southern stocks for some years. However, the degree and direction in which these parameters would be changed cannot be known since the number of animals moving during ENSO events or

which stock they are coming from are not known. Removal of samples collected during ENSO years could limit this potential bias. However, this would reduce sample size by hundreds and would not be recommended unless additional data become available to support the hypothesis that *D. delphis* stocks mix during ENSO events.

CHAPTER 6: CONCLUSIONS

The goals of this study were a) to determine if age estimations of delphinid teeth could be improved or maintained using enhanced digital imaging, b) to describe the growth and reproduction of central female *D. delphis*, and c) to determine whether spatial and or temporal trends in total length and calving season of central females were apparent in the ETP (potentially reflecting finer scale population structure).

My comparison of precision and bias between two aging platforms (Chapter 3) provided encouraging results for using digital imaging for aging but also pointed to inherent flaws in the protocol that require further investigation. Precision of age estimates obtained using the compound microscope and the image analyzer were comparable. However, age estimates of older animals were lower for one reader when using the image analyzer. This likely occurred because the reader did not consistently use higher objective images to read the last group of GLGs. Replicate experiments with new readers and improved protocols are currently being conducted to determine whether this bias can be resolved. If this bias can be eliminated, the image analyzer would serve as an excellent tool in archiving and reading delphinid teeth.

Analyses of growth and reproductive parameters show that central female *D. delphis* (Chapter 4) have different life history characteristics than their conspecifics in the North Pacific and from the closely related *Stenella* spp. in the ETP. Geographic variation in the North Pacific appears to occur in *D. delphis*, with longer individuals and year-round breeding found in the south. Central *D.*

delphis also appear to be unique in comparison to the closely related *Stenella* spp. in the ETP because they have a calving interval that is approximately one year shorter. This is likely due to the greater number of females that lactate while pregnant. *D. delphis* may be able to handle the increased energy demands of lactating while pregnant due to the upwelling modified habitat that they inhabit which likely provides a richer food source than the relatively unproductive areas that *Stenella* spp. inhabit.

Several caveats to life history parameter estimations associated with fishery sampling were noted during the analysis of growth and reproduction and alternative estimates were presented based on these caveats. ELB could be overestimated by 3.4 cm due to undocumented calf mortality, ASM could be underestimated by two years due to “missing” immature animals in the sample, and calving interval could be underestimated by a factor of 1.7 due to high fetal mortality possibly associated with repeated chase and capture in the fishery. These alternative estimates must be considered if these parameters are to be used in population modeling for this species as well as other species impacted by the same fishery.

The spatial and temporal analysis (Chapter 5) showed that central *D. delphis* habitat varies, and although evidence for finer scale population structure was not found, there was evidence that animals may move considerable distances and possibly cross stock boundaries in response to changes in habitat. The mean total body length of *D. delphis* sampled “on” the Costa Rica Dome was 10 cm shorter than those sampled “off” the Costa Rica Dome during the years 1973-74.

However, no difference in mean total body length between the aforementioned spatial groups was apparent in the “later” years of 1988-89. The difference between spatial groups within the central stock during the 1973-74 time period might be attributed to shorter southern stock *D. delphis* moving into the higher quality habitat of the Costa Rica Dome area during the strong El Niño of 1972-73 when preferred habitat was likely reduced in the south. There is no evidence for finer scale population structure in central female *D. delphis* in the data analyzed, and the most likely explanation of results point to a temporary distribution shift of animals rather than a biological difference between animals “on” and “off” the Dome.

In summary, image analysis appears to be a promising tool for aging delphinid teeth that needs to be explored further. There is no evidence for fine scale geographic variation in life history within the central stock, although individuals appear to cross stock boundaries in response to environmental change. Furthermore, large scale geographic variations in life history characteristics of *D. delphis* in the North Pacific was documented with longer individuals and year-round breeding found in the tropics.

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APPENDIX: LIST OF ABBREVIATIONS

APR	annual pregnancy rate
ASM	age at attainment of sexual maturity
CHL	surface chlorophyll concentration
DIST	distance from shore
ELB	estimated length at birth
ENSO	El Niño-Southern Oscillation
ETP	eastern tropical Pacific
GLG	growth layer group
LSM	length at attainment of sexual maturity
MMPA	Marine Mammal Protection Act
NEC	North Equatorial Current
NECC	North Equatorial Counter Current
NMFS	National Marine Fisheries Service
PCA	principal components analysis
SEC	South Equatorial Current
SECC	South Equatorial Counter Current
SEM	scanning electron microscopy
SST	sea surface temperature
SWFSC	southwest fisheries science center
THERM	mean thermocline depth
Z20	20 °C isotherm depth